

Title	Habitat preferences and movement patterns of bottlenose dolphins at various spatial and temporal scales
Authors	Garagouni, Maria
Publication date	2019
Original Citation	Garagouni, M. 2019. Habitat preferences and movement patterns of bottlenose dolphins at various spatial and temporal scales. PhD Thesis, University College Cork.
Type of publication	Doctoral thesis
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Download date	2023-05-05 11:39:30
Item downloaded from	http://hdl.handle.net/10468/8618

Habitat preferences and movement patterns of bottlenose dolphins at various spatial and temporal scales

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A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy

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School of Biological, Earth, & Environmental Sciences

University College Cork

2019

ἐν ποιήμασι τῶν χειρῶν σου ἐμελέτων



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DECLARATION

I hereby declare that the work presented in this thesis is my own unless explicitly stated otherwise and that it has not been previously submitted for another degree at University College Cork or elsewhere.

AN EXPLANATORY NOTE ON THE TEXT

The data chapters herein were written with the intention of submitting them to peer-reviewed journals for publication. For this reason they are formatted as article manuscripts, and as such there is a certain amount of repetition between chapters, particularly in the introductory sections. The authors of each manuscript are listed at the beginning of each chapter, as they will be upon publication, based on their contribution to each article. The contribution of authors besides myself and my supervisors are specified at the start of each chapter.

ACKNOWLEDGEMENTS

In science, as in life, achieving things is down to hard work. But it's also down to the people around you. And it's often also down to a little bit of luck. I know I've worked hard to get to this point, but I've also been extraordinarily lucky in having the right people around me. And this is where I get to thank you, on the record. Here goes.

First of all, of course, my supervisors. Emer Rogan, for your unwavering support, guidance, encouragement, and kindness from the very beginning, when I was trying out models for the first time as a master's student, to the very end. Thank you for giving me the chance to do this, and for being an incredible supervisor. Simon Ingram, thank you for the long-distance support and for all the advice and enthusiasm throughout this project. Hopefully my emails to you both from now on will always sound less frantic than in the last few months.

Next, Milaja Nykänen, for showing me the way, as it were. I cannot thank you enough for all your support, for always answering my endless questions about oh-so-many issues and non-issues. For teaching me photo-ID, for sharing all your practical tips on how to do everything that much quicker, for being the sweet, patient voice I needed to hear when the data drove me up the walls. You are marvellous and I want to be like you when I grow up.

Enrico Pirotta, your ability to take the tangled mess of thoughts in my head and formulate coherent questions before I could express what I didn't understand will never cease to amaze me. Thank you for your patience and your invaluable modelling advice. I still owe you a Greek dinner.

Mary Kate Bolger, my 'wondergrad' fieldwork assistant, logistics queen, dolphin identifier extraordinaire, sharer of confined quarters, provider of comfort and comfort food, dryer of tears and holder of hands through the tough parts, first of her name...no, wait, I'm getting carried away. Except there really is no limit to what I could say in thanks for everything you've done for me and continue to do.

Geoff and Susanne (and Minnie!) Magee, thank you for letting me use your magical boat (pun very much intended) for two whole summers. Thank you for showing me the ropes on the *Draíocht*, for taking care of Mary Kate and me in our little clifftop home, for all the drives and laughs and knowledge and stories shared. I'll be back soon, I promise.

The Cooperage crowd, old and new, thank you for making postgrad life a constant source of fun. You really are the BEES Knees. Special shoutout to Anthony Caravaggi, Emma Critchley, Adam Kane, and Saskia Wischnewski, for coding and mapping advice.

In no particular order because there is no ranking you in my heart, Kerstin Klingler, Seán MacGabhann, Rosemary Murphy, Maeve O'Connell, Lucy Taylor, if you don't know how much you mean to me and how grateful I am for your collective existence in my life by now, then I've been doing it wrong. Sean and Kerstin, Wine Time?TM was and is the greatest institution ever founded—here's to it lasting forever! Maeve and Ro, if I didn't love you so much, I'd be mad at you for moving so very far away from me before I finished this, but I can't hold it against you, because you still pelted me with love and support from a distance. Lucy, apart from encouraging my orotund—bordering sometimes on magniloquent—ramblings and all the thoughtful little kindnesses, and taking care of Larry in my absences, you get special thanks and kudos for putting up with me in the final, most stressful months.

Jacopo Di Clemente, you may hate me for this, but you know exactly what you've done, so I won't let it go unacknowledged.

Mom and Pa, John, Costy, Steph, Anna, Γιαγιά, and Fr Κάλλιστος, thank you for making me who I am. I owe you my sense of self and self-worth, my ability to think, work hard, communicate, laugh, cry, and generally get through things, knowing you'll always have my back—even if it's to give me a kick in the behind when I need it. I would not be here without you and I hope you know my impending job insecurity is all your fault for educating me and encouraging me to follow my dreams.

Larry-cat, I know you can't read and probably don't care, but adopting you was the best impulsive decision I ever made. Thank you for choosing me when I came to the shelter and thank you for keeping me sane and preventing me from working overtime.

My PhD scholarship was generously funded by the Bodossaki Foundation.

Funding and support for the ObSERVE aerial surveys was provided by the Department of Communications, Climate Action & Environment and the Department of Culture, Heritage & the Gaeltacht. We are grateful to the team at Aerostravia, Jean-Philippe Pelletier and pilots Romain Fert, Laurent Pellicer, Aurelien Bidot, Paul Rameau, Pierre Maillard, and engineer Noel Bar. We would also like to thank the observers and data-loggers Ash Bennison, Nick Richardson, William Hunt, Milaja Nykanen, Hans Verdaat, Nicole

Janinhoff, and Ailbhe Kavanagh and our steering group, Prof. Phillip Hammond, Dr Mark Tasker, Dr Meike Scheidat, and Prof. Vincent Ridoux.

University of Plymouth provided the C-PODs used in the passive acoustic monitoring study. We would like to thank Breffni and Cillian Gray of Scubadive West and Brian Graham for assisting with C-POD retrieval and maintenance, as well as the School of BEES for additional funding.

The surveys of the Shannon Estuary in 2015 were funded and licensed (License No. 107/2015) by the Irish National Parks and Wildlife Service. We would like to thank Oliver Ó Cadhla for his support. We would also like to thank Luke Harman, Mick Mackey, Seán MacGabhann, and Patricia Breen for help with fieldwork, and Mary Kate Bolger for assisting with photo-identification.

ABSTRACT

Quantifying marine mammal abundance, site occupancy, and habitat use patterns is fundamental for the correct design and implementation of conservation and management schemes. Bottlenose dolphins in Irish waters form at least three distinct populations, two coastal and one pelagic, each ranging in different areas over unequal scales. While the abundance of all three has been estimated and core areas of use have been previously identified for the coastal populations, their habitat preferences have not yet been investigated sufficiently.

In this thesis, generalised additive models were used to describe the habitat use of each population in relation to a suite of static and dynamic environmental parameters, over a range of temporal scales. Mixed models and generalised estimating equations were implemented to account for spatial and temporal autocorrelation when necessary.

The habitat use of the pelagic population was modelled using two seasons (Summer and Winter) of aerial survey data of the greater part of the Irish EEZ and the models' predictive capacity was tested on observations from two separate seasons. The interaction of environmental covariates with a habitat classifier was also tested to elucidate dolphin habitat use changes depending on whether they are in shelf, slope, or abyssal waters.

The site occupancy of the coastal mobile population was modelled using five years of passive acoustic monitoring (C-POD) data from two locations on the west coast at an hourly, daily, and monthly scale. The second coastal population is resident in the outer Shannon estuary Special Area of Conservation and its abundance has been sporadically monitored for nearly two decades using boat-based photo-identification surveys. Encounter data from these surveys were used to model habitat use by incorporating a two-dimensional geographic coordinate term and an interaction with tidal phases. Given the irregular frequency of standardised surveys, I also assessed the potential of using a dolphin-watching boat operating in the same area as an alternative platform from which to derive a robust abundance estimate, using mark-recapture techniques.

Different environmental covariates proved significant at each spatial scale, with dolphins showing season-, habitat-, and site-specific responses to each parameter. A higher probability of dolphin presence was predicted over the continental shelf and slope in the winter and in two primary areas in the summer, the southwest coast and the Porcupine Basin. Sea surface temperature and primary productivity were significant predictors of

dolphin presence for both the pelagic and mobile coastal population, but not for the resident coastal population. Tidal level had a significant effect on dolphin detection in the coastal mobile population, with the likelihood of detections increasing at higher water levels. Tidal phase was also a significant predictor of dolphin presence for the resident population, with higher probabilities being predicted closer to a bottleneck feature during ebb tides.

The abundance estimate generated from the dolphin-watching boat observations compared favourably to an estimate generated from a standardised survey the previous year. This indicates that, in years when standardised surveys do not take place, the dolphin-watching boat may provide a suitable interim platform for more frequent and efficient monitoring of this population.

The results presented here highlight the importance of investigating habitat use at different spatial and temporal scales, provide valuable insights regarding areas used at different times by bottlenose dolphins, and form a baseline upon which to build further, more targeted investigations of the habitat preferences, demographic parameters, and abundance of each population, ultimately advancing our efforts at conservation and facilitating marine spatial planning.

Chapter 1. GENERAL INTRODUCTION

Aristotle was not only the first scientist to correctly define cetaceans as mammals—he grouped the whales into toothed and baleen, and estimated the lifespans of dolphins and sperm whales—but he also described organisms in terms of the habitat they occupied, believing that this was an integral part of their very essence (Gelber, 2015). Today, one of the cornerstones of conservation biology is to understand how organisms interact with their environment; knowing what resources a species relies on and which habitats are fundamental to its survival is a critical component of minimizing human disturbance. With mobile organisms, such as marine mammals, studying their movement patterns gives us insight into what their requirements are regarding food, shelter, and the ability to reproduce. Due to the generally patchy distribution of resources in naturally occurring ecosystems, the animals that rely on them are also not uniformly distributed throughout their range (Aarts et al., 2013). Knowing which elements of their habitat drive these movements allows us to better target our conservation and management efforts.

1.1. Cetacean conservation

Globally, cetaceans face a number of pressures from human activities, directly and indirectly. These include marine pollution, with some marine mammal species showing dangerously high contaminant loads (e.g., Desforges et al., 2018), noise disturbance (e.g., Erbe et al., 2018), vessel traffic (e.g., Bejder et al., 2006), and climate change (MacLeod, 2009).

There are several different bodies and regulations which act as reference points for marine mammal conservation efforts. The International Union for Conservation of Nature (IUCN) classifies species and populations according to their risk of extinction. Of 89 cetacean species listed in 2017, 20% were assigned to a “threatened” category (Critically Endangered, Endangered, Vulnerable, or Near Threatened), while almost 50% were classed as “Data deficient” (IUCN Cetacean Specialist Group, 2017). Most delphinid species are also listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), regulating their commercial trade in countries that have signed the treaty. Moreover, the European Habitats Directive (92/43/EEC) lists all cetaceans under Annex IV, requiring EU member states to “strictly

protect” such species. Common bottlenose dolphins (*Tursiops truncatus*), hereafter referred to as bottlenose dolphins, are also listed in Annex II of the Habitats Directive, necessitating the designation of Special Areas of Conservation (SACs) by member states to maintain or restore a “favourable conservation status” for the species. Another EU directive, the Marine Strategy Framework Directive (MSFD, 2008/56/EC), applies an ecosystem-based approach to the management of human activities in the marine environment; bottlenose dolphins are top predators and so considered indicator species of “good environmental status” in coastal waters for this purpose.

In order to quantify the health or, indeed, the extinction risk of a cetacean population and thus fulfil our requirements towards maintaining a healthy conservation status, it is fundamental to understand the animals’ needs. This includes identifying their habitat use patterns and whether these change over time, which elements of their environment are the limiting or driving factors of their occurrence, and how many individuals (and of what age/reproductive capacity) there are within any given population. Addressing these questions by observing animals that are only visible for short spaces of time, during favourable weather and in good light, often over a very wide range, is a challenging task.

1.2. Bottlenose dolphins and their distribution in Irish waters

Bottlenose dolphins are a cosmopolitan cetacean species, found in all but the polar regions of the world’s oceans (Jefferson, Webber, & Pitman, 2015). In the Pacific, they do not normally occur above 41°N (Bearzi, Saylan, & Hwang, 2009), although there was a sighting of 200 animals at 50°N in 2017 (Halpin, Towers, & Ford, 2018). In the Atlantic, they have been recorded as far as 69°N near the Lofoten islands (Wells & Scott, 2009). They occur in open waters, as well as close to coastlines, and even within estuarine systems. Globally they are listed as “Least Concern” by the IUCN, although some populations are “Vulnerable” (www.iucnredlist.org). The original description by Montagu (1821) was based on the skull and teeth of an animal caught for exhibition (and subsequent conversion to oil). Their life history, morphology, physiology, and diet were originally gleaned from animals that were killed (True, 1890) or caught and kept in captivity, while their distribution and abundance was inferred from ship-based and land-based observations (True, 1890; Miller, 1923).

Today, dolphin populations can be studied from boat-based or aerial platforms, through land-based surveys for coastal populations, or through tagging. Their movements can be tracked using the GPS waypoints of moving platforms, in combination with distance and angle measurements, or using surveyors' theodolites from land. Bottlenose dolphins can also be individually identified through the accumulation of markings (nicks, notches, and rake marks acquired through interactions with conspecifics, predators, or vessels and nets) on their dorsal fins and bodies (Würsig & Würsig, 1977). Individual markings make photo-identification and mark-recapture (or capture-recapture) estimates of abundance possible, as well as giving us the ability to monitor a population over time and learn its demographic characteristics. Bottlenose dolphin diet has long been known to be varied, consisting of benthic and pelagic fishes and invertebrates, depending on their location (Gunter, 1942). Diet data are collected through stomach content analysis of stranded, bycaught, or intentionally killed animals, as well as through observations in the field, faecal samples, and stable isotope analysis (Dunshea et al., 2013; Wells et al., 2013; Rossman et al., 2015).

It is also possible to study cetacean occurrence acoustically, with the use of hydrophones that detect their echolocation clicks or other vocalisations; these hydrophones can be stationary, to study occupancy patterns in a particular region, or towed behind vessels, for detection of the animals in a wider area (Janik, 2000; Praca et al., 2009; Soldevilla et al., 2011; Booth et al., 2013; Wells et al., 2013; Squires et al., 2014). It is currently difficult to impossible, however, to ascertain group sizes or identify individuals through acoustic methods alone, so they are generally used as a proxy measure for the presence of a species in the study area. A drawback of acoustic monitoring is that the animals have to be echolocating (or otherwise vocalising) in order to be detected. The benefit of acoustic monitoring, however, is that it is not limited to daylight hours and favourable weather conditions, or by the animals' surfacing patterns, as there is no visual component to the data. Stationary arrays are relatively cheap to maintain once the equipment is deployed. A further advanced application is the use of autonomous mobile 'gliders' that move with ocean currents and make acoustic recordings over a much wider area, without the logistical or financial restrictions of having to manually tow them (Klinck et al., 2012; Davis et al., 2016).

In the Northeast Atlantic, genetic analyses have shown a hierarchical structure of bottlenose dolphin populations, namely, a pelagic and coastal population, which are

further divided into the Pelagic Atlantic, Pelagic Mediterranean, Coastal North, and Coastal South populations (Louis et al., 2014a; 2014b). In Irish waters, bottlenose dolphins are known to occur year-round, in both coastal and offshore waters. At least three distinct populations have been identified, based on genetic and photo-identification studies (Mirimin et al., 2011; Louis et al., 2014a; Oudejans et al., 2015; Nykänen et al., 2018). One population is resident within the Shannon Estuary, displaying high site fidelity, low genetic diversity, and exhibiting genetic isolation from other populations, aside from a small group of animals observed in Cork Harbour with which they appear to be linked (Mirimin et al., 2011; Nykänen et al., 2018). They are one of the qualifying species for which the Lower Shannon Estuary SAC was designated in the early 2000s. However, the SAC does not cover their entire known range, as photo-identification has shown some animals in nearby bays (Levesque et al., 2016) and at least one animal has been sighted as far north as Donegal (Nykänen, 2016). The size of the population has long been monitored using mark-recapture surveys, the latest estimate being approximately 139 individuals (Rogan et al. 2018).

Another population ranges along the west coast of Ireland, although the precise extent of its range is unknown. Nykänen et al. (2015) used a Bayesian multi-site mark-recapture approach to estimate the population's size and found it to be 189 individuals in 2014. These animals appear to be genetically linked to other coastal populations in the UK, being part of the larger Coastal North population (Louis et al., 2014a). The link with other groups of the Coastal North population may also be demographic—one of the dolphins identified in Donegal in 2014 had previously been sighted in the Inner Hebrides in 2004 and the Moray Firth, Scotland, in 2001 (Robinson et al., 2012). The large number of neonates and calves observed in specific areas of the west coast resulted in the designation of another, multi-site SAC in 2013 (West Connacht Coast SAC), as they are considered important calving sites.

The high genetic diversity found in some stranded bottlenose dolphins led Mirimin et al. (2011) to conclude that they originated from a third population ranging in the open waters beyond the Irish coast. This is further supported by Louis et al. (2014a, 2014b), whose study of genetic markers clustered all coastal bottlenose dolphins in the UK and Ireland into a single population and suggested that these are distinct from the Pelagic Atlantic ecotype. Moreover, Oudejans et al. (2015) concluded that the bottlenose dolphins on the west coast of Ireland are socially distinct from those using offshore waters. Very little is

known about the pelagic population, with no delineation of its range beyond the continental slope. A genome-wide (nearly 800,000 SNPs) comparison of pelagic individuals from the Eastern and Western North Atlantic shows that they form distinct populations, but show lower genetic differentiation than that between coastal and pelagic ecotypes in either region (M. Louis, pers. comm. 2019). Large-scale marine megafauna surveys have estimated the abundance and density of bottlenose dolphins in the Northeast Atlantic at various times and found them to be anywhere between ~16,400 and ~27,600 individuals (SCANS I, II, III, CODA). Within the Irish EEZ, a two-year aerial survey programme showed their abundance to be between ~12,000 individuals in the summer of 2015 and ~212,000 animals in the winter of 2016 (Rogan et al. 2018).

1.3. Habitat use and generalised additive models

Species distribution models use statistical regression, profiling, or machine learning techniques to describe the patterns in occurrence of a species or population in relation to the physical environment (Elith & Leathwick, 2009). They are used extensively to study the habitat preferences of marine mammals (Ballance, Pitman, & Fiedler, 2006; Becker et al., 2016; Gregr et al., 2014; Redfern et al., 2006). Their primary applications include determining the environmental factors that drive animal movement patterns, investigating historical species distributions, and predicting future distribution patterns (Boyd et al., 2015; Johnston, Thorne, & Read, 2005; Lambert et al., 2018; Lambert et al., 2014). Through such habitat models, we have gained invaluable insight into the ecology of multiple cetacean species (Bombosch et al., 2014; Correia et al., 2015; Ferguson et al., 2006; Thorne et al., 2012; Lambert et al., 2014; Rogan et al., 2017; Lambert et al., 2018). Such knowledge is crucial for the development of appropriate conservation and management schemes of these mobile top predators (Cañadas & Hammond, 2008; Embling et al., 2010; Panigada et al., 2008).

Several types of models have been developed over the past few decades, depending on the quality of data gathered and the questions being addressed. That is, the goal might be to describe the patterns of occurrence relative to environmental variables or to elucidate the precise link between these ecological drivers of occurrence, or to predict the species distribution to a time or place extending beyond the study period and area. Given the limitations of cetacean surveys, i.e., the fact that the animals are not always visible or audible, the lack of cetacean sightings from any visual platform (or acoustic detections

from an acoustic one) cannot be taken as conclusive proof that no cetaceans are present. Therefore, the type of data collected for such models is generally classed as presence-only, presence-absence, presence-background, or occupancy-detection data (Guisan & Zimmermann, 2000; MacKenzie et al., 2003; Pearce & Boyce, 2006; Aarts, Fieberg, & Matthiopoulos, 2012). Ultimately, the unifying theme of habitat models is their aim to quantify the probability of an organism occupying a specific site at any given time. However, the probability of recording a dolphin's presence in a site depends not only on whether the species occupies that site, but also on whether the site is sampled and whether the animal is observed (Guillera-Arroita et al., 2015). Therefore, biases can be introduced by poor study design, logistical limitations, and the observation constraints mentioned previously.

A commonly used modelling technique in the marine mammal world is generalised additive modelling (GAM). GAMs are an expansion of linear regression models, with two very attractive features: they do not assume a normal distribution of data and they use smoothing splines that, cumulatively, capture non-linear responses to predictor variables very effectively (Hastie & Tibshirani, 1987). Given the constraints described above in marine mammal observations, the highly flexible nature of some cetacean species, and the dynamic nature of the marine environment, non-normal distributions are a recurring theme in cetacean habitat modelling. The flexibility of GAMs allows them to detect non-linear relationships with environmental covariates and, if applied carefully, without incorporating too much noise from any given dataset (i.e., over-fitting) (Matthiopoulos & Aarts 2011). However, they are still subject to statistical constraints and biases, some of which are outlined below and in the subsequent chapters.

The scale of a study may bias the outcome of a model, both in relation to the study species and the environmental covariates used. Scale plays a very important role in the accuracy of regression-based models, at the level of both the extent of a study and the resolution of the data collected (Austin, 2007). For instance, the extent of the study area should range beyond the observed upper and lower limits of the species' occurrence. Otherwise, the species' responses are truncated and that affects the shape of the response curve. Different habitat variables may affect the population in question at different scales (Palacios et al., 2014). For example, water temperature and salinity may constrain a cetacean species within certain geographical limitations, but, on a regional scale, the availability of prey depending on localised currents, upwellings, substrate types, etc., may play a much more

important role in their fine-scale movements (Bailey & Thompson, 2010; Doniol-Valcroze et al., 2012; Nuuttila et al., 2017).

Choosing the right predictors to include in a model can be difficult. According to Austin (2007), predictor selection is generally done on one of three bases: knowing the biophysical processes that might drive distribution, knowing the ecophysiological processes that may do the same, or knowing that the variables chosen can act as proxies for the real drivers, through the experience that they show correlation with species distributions. To illustrate the latter approach, it is fairly common when studying marine mammal distributions to use primary productivity as a predictor, even if the study species feeds on a higher trophic level, because the chlorophyll content (and therefore plankton abundance) of the water acts as a surrogate for the actual prey distribution (e.g., Pirotta et al., 2011; Roberts et al., 2016). While prey distribution is a highly desirable predictor, it is often practically impossible to get accurate measures thereof in the marine environment (e.g., Torres, Read, & Halpin, 2008; Hazen et al., 2011). Furthermore, predator distributions are not likely to closely match those of their prey unless the animals are constantly focused on areas with the highest prey densities. In fact, non-foraging activities such as migrating, socialising, or breeding also influence species' movements and distributions (Rasmussen et al., 2007; Blasi & Boitani, 2012; Keller et al., 2012).

Another challenge in regression-based habitat modelling is to account for the autocorrelation of observations. GAMs calculate the significance of each predictor based on the assumption that there is no spatio-temporal correlation in model residuals (Wood, 2017). If positive correlation is not taken into account, the model is likely to falsely identify significant effects when there are none. This is especially problematic if there are patterns in the data that the predictors included in the model cannot explain, as it leads to “overconfident model results” (Mackenzie et al., 2013). Both spatial and temporal correlation in observations of marine megafauna are common, given the persistence of prey patches around static landscape features or frontal systems, as well as the often linear shape of survey transects and the serial recording of data in passive acoustic surveys. Autocorrelation can be accounted for in GAMs by “thinning” the dataset by means of dropping observations until the remaining ones are independent, by specifying a correlation structure in a mixed effects model, or through the use of generalised estimating equations (GEEs). In GEEs, appropriate temporal or spatial blocks of data are identified, within which autocorrelation is specifically modelled and between which independence is

assumed (Liang & Zeger, 1986). When combined with the flexibility of additive models, this approach can be extremely powerful in identifying non-linear effects without compromising statistical integrity or forcing us to discard observations (e.g., Pirotta et al., 2011).

It is important to note that the habitat preferences (the ratio of use over availability of any given habitat) of a species may not necessarily reflect the driving factors of that species' movement patterns. An animal may occur in a given location because it is geographically and physiologically available to it, but we cannot understand the importance of that location without knowing why the animals are attracted to it. That is, some environments may be visited frequently by a mobile animal because they are readily available, while some others may only be occupied infrequently or for short periods, but without knowing the reasons (i.e., whether they are critical for reproduction, shelter, food, or actually inhospitable) we cannot say with any confidence that those locations are not necessary for the species' survival (Matthiopoulos & Aarts, 2011). Nevertheless, quantifying the likelihood of a species' occurrence anywhere is a crucial first step to understanding its habitat needs. This knowledge can then be built upon with the inclusion of behavioural data, to elucidate why the animals are found where they are.

1.4. Abundance estimation

An essential first step towards being able to protect an animal population is to know how many animals are in it. Without that, it is difficult to be certain that conservation measures are having any effect. Depending on the range and movements and behaviour of the animals in question, it is not always possible to get a precise count. For marine mammals this is exceptionally challenging, due to the aforementioned limitations in actually observing them. As a result, various modelling approaches have been developed to address the issue. One approach is to evenly and randomly sample as large a range as possible of the species in question, using line transect survey methods, and calculate the density of animals in the region based on the number of detections per unit of effort (Hammond et al., 2002; Barlow & Forney, 2007; Lewis et al., 2007). Acoustic abundance estimates may also be generated from fixed sensor arrays (Marques et al., 2009; Küsel et al., 2011), depending on the rarity and behaviour of the species in question (Mellinger et al., 2007); however, for most species, getting accurate measures of group size based solely on vocalisations or echolocation clicks is exceedingly difficult.

For bottlenose dolphins, which are identifiable through photo-identification, mark-recapture abundance estimates have long been in use (Würsig & Würsig, 1977, Urian et al., 2015). Mark-recapture surveys are based on sampling representative samples of the population over a series of sampling or “capture” events (Otis et al., 1978). The assumptions of mark-recapture abundance estimates are further detailed in Chapter 5. It is easier to apply this method to coastally ranging populations than to offshore populations, although there are still multiple logistical and financial constraints there, depending on the remoteness of the study areas and the availability of resources. Given these constraints, the mobile population on the west coast of Ireland has only been surveyed twice. The resident population in the Shannon Estuary SAC has been surveyed more often, but at irregular and infrequent intervals, predominantly to meet statutory requirements. It is, therefore, worth investigating the potential of alternative survey methods to augment standardised surveys.

1.5. Thesis outline

The aims of this thesis, summarised in Figure 1.1, are to investigate the habitat use of three discrete bottlenose dolphin populations in Irish waters, to investigate how similar environmental parameters affect each population on a different scale, and to assess an alternative platform from which to estimate the abundance of a resident population.

Chapter 2 addresses the question of seasonal habitat use in the pelagic dolphin population. It includes developing GAMs to identify habitat use patterns and testing the explanatory and predictive power of the final models.

Chapter 3 investigates the site occupancy patterns of the mobile coastal population, using long-term passive acoustic monitoring data. GEE-GAMs are used to model covariates on three temporal scales.

Chapter 4 explores the habitat use of the resident coastal population in the Shannon Estuary. GAMs are used to determine the relationship between dolphin occurrence and static and dynamic environmental features.

Chapter 5 assesses the potential of a dolphin-watching boat to be used as a platform of opportunity to monitor the abundance of the resident coastal population. Mark-recapture techniques are applied and the minimum amount of survey effort required to obtain a robust estimate is calculated.

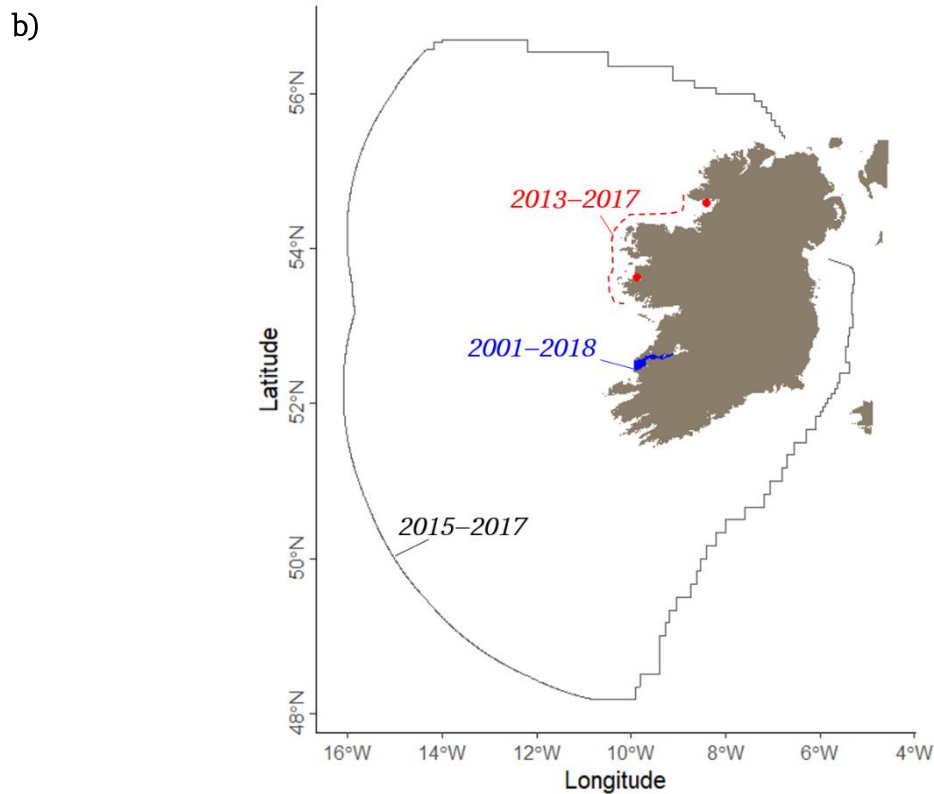
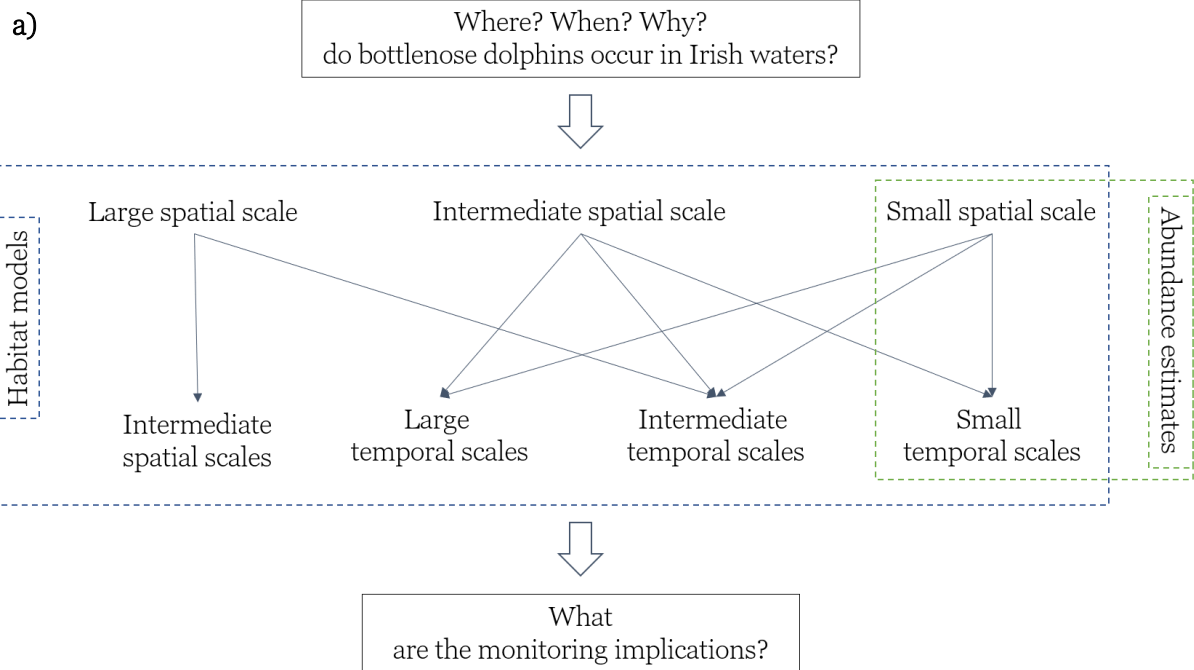


Figure 1.1. a) Conceptual map of the questions addressed in this thesis regarding the distribution and monitoring of bottlenose dolphins in Irish waters. b) Illustration of the scales at which these questions were investigated. Grey line: Irish EEZ. Blue: Shannon Estuary study area. Red: Passive acoustic monitoring sites. Dates indicate the temporal range covered by each dataset.

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Chapter 2. Habitat use of bottlenose dolphins on the northeast Atlantic margin

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Author contributions:

1. Advice on use of models, model selection, and R packages.
2. Calculation of Effective Strip Width and processing of environmental data.
3. Processing of environmental data.
4. Partly in charge of sighting data collection

ABSTRACT

In order to design adequate conservation and management schemes for cetacean populations, it is fundamental to understand how their habitat use varies throughout their range and at different spatial and temporal scales. In the Northeast Atlantic, a genetically distinct pelagic population of bottlenose dolphins has been identified, but the habitat use patterns of these animals are not known. Using data from aerial surveys, we developed generalised additive models (GAMs) to investigate how dolphin presence and numbers relate to static and dynamic environmental parameters. Two sets of binomial models were run; the first included all covariates, while for the second, habitats were classified as being on the continental shelf, slope, or abyss, and this was included as an interaction term with the other covariates. GAMs were trained using the latter two survey seasons and their goodness of fit was tested on concurrent data, while their predictive capacity was tested on data from the first two seasons. Quasi-Poisson GAMs were also run to test whether the number of dolphins sighted was affected by the same environmental variables as their presence. The results show that sea surface and bottom temperature, mixed layer depth, primary productivity, and seabed aspect and rugosity all play a significant role in bottlenose dolphin distribution, as did proximity to the coastline and various depth contours. However, the significance and effect of most variables differed between habitat types and between seasons. The models predicted higher probability of dolphin occurrence near the southwest coast in the summer and throughout most of the continental shelf in the winter. This baseline study of bottlenose dolphin habitat use in the Northeast Atlantic can be used to inform future targeted studies of this pelagic population.

2.1. INTRODUCTION

The development of appropriate conservation plans for mobile animal species needs to be underpinned by a thorough understanding of how they move within their environment to meet their needs (Wallace et al., 2010; Maxwell et al., 2013; Dransfield et al., 2014). Moving between various habitat types for different purposes leads to the development of habitat use patterns, or habitat preferences (Garshelis, 2000). Habitat preference can be defined as the ratio of use over availability of a given habitat; that is, all habitats being equally available, the ones that are actually used most are the ones “preferred” by the animals (Johnson, 1980). These preferences are determined both by the biological characteristics (life history, foraging strategies, physiological constraints) of the animals in question and by the existence within their environment of sufficient resources, such as prey and shelter, and threats including predators and competition, which ultimately determine the distribution of the species (Morris, 2003).

Habitat use models have long been used as a tool to investigate these preferences, often under the term ‘species distribution models’ (Austin, 2007; Redfern et al., 2006; Redfern, et al., 2008; Robinson et al., 2011). Habitat models link a measure of the species’ usage of each habitat type—generally its presence in or absence from an area, or its density within that area—to environmental variables comprising that habitat type (Peterson, 2001). Such models can be explanatory, describing the patterns observed within the study area in a specific time period, or predictive, extrapolating those patterns beyond the study limits in space and/or time (Elith & Leathwick, 2009; Morley et al., 2018). Theoretically, a perfect model will capture all the complexities in the relationship between species and environment and be able to accurately describe both the observed data and to predict distribution patterns for other regions or periods. In practice, however, there is a trade-off between the model fitting the data closely enough to have a meaningful interpretation and loosely enough to not be affected by noise (over-fitting), so it is often difficult to achieve a model that is both explanatory and predictive (Mac Nally, 2000).

According to Robinson et al., (2017), species distribution modelling for the marine environment is a relatively new field that has grown considerably in the past decade. Many different types of habitat models have been developed, each of which deals with different modelling constraints and biases. For marine megafauna, a frequently used approach is with generalised additive models (GAMs) (e.g., Forney, 2000; Ferguson et al., 2006; Forney et al., 2012). These models show considerable flexibility in their assumptions

regarding the data and in their ability to capture non-linear relationships with predictor variables. They do this by generating smooths of additive functions that incorporate the principal features of the data (Matthiopoulos & Aarts 2011) even if very little is known about the underlying mechanisms that generate observations (Guisan, Edwards, & Hastie, 2002). GAMs can be used with binary (i.e., presence/absence) or count (e.g., group size) data, as well as with discrete or continuous predictors (Redfern et al., 2006).

For marine top predators within their entire distribution range, the only physical restriction to their movements is the presence of landmasses, while temperature, for example, can impose a physiological restriction. Allowing for differences between life stages and reproductive status (e.g., Pack et al., 2017) cetacean distribution depends largely on the availability of prey resources. As data on dietary preferences and prey availability are often insufficient, abiotic factors are generally used as proxies to describe and predict a species' distribution (Cañadas, Sagarminaga, & García-Tiscar, 2002; Eierman & Connor, 2014). Such proxies include latitude, longitude, and depth, which are especially context-dependent, but can be useful because they often follow other driver gradients (McArthur et al., 2010). Other variables, such as rugosity, have stronger independent predictive power, especially for benthic prey communities (Maravelias 2011, Ferrari et al. 2017). Surface and bottom temperatures, mixed layer depth, and surface chlorophyll concentration relate to primary productivity, and the availability of fine-scale satellite measurements of these variables make them widely used environmental predictors in marine modelling (Palacios et al., 2006; Mannocci et al., 2014; Gomez & Cassini, 2015; Scales et al., 2015). The indirect links between such proxies for potential prey distribution and their effect on top predators introduces an extra layer of uncertainty to habitat models, which can impact both their explanatory and predictive power.

Common bottlenose dolphins (*Tursiops truncatus*) are a cosmopolitan marine top predator inhabiting pelagic, coastal, and estuarine waters throughout temperate and tropical regions (Leatherwood & Reeves, 1990). Although globally the taxonomy is not clearly defined, in the Northeast Atlantic, there appear to be multiple genetically discrete populations, some of which are resident in bays and estuaries, while others range further from shore (Wilson et al., 1997; Ingram & Rogan, 2002; Mirimin et al., 2011; Cheney et al., 2013; Louis et al., 2014; Arso Civil et al., 2019). In the waters around Ireland, genetic and photo-identification evidence suggests that there are at least three distinct populations, one resident within the Shannon Estuary, one ranging along the west coast,

and one “pelagic” population, the full range of which has not yet been established (Mirimin et al., 2011; Louis et al., 2014; Oudejans et al., 2015; Nykänen et al., 2018).

Bottlenose dolphins are listed in Annex II and Annex IV of the European Habitats Directive, meaning that EU member states must sustain their favourable conservation status through conservation and management plans, done largely through the designation of Special Areas of Conservation. To achieve this effectively, knowledge on their precise distribution and habitat preferences is fundamental. However, although there have been several large-scale surveys within the Northeast Atlantic to determine their abundance and density (SCANS II, 2008; SCANS III, Hammond et al., 2017; CODA, Hammond et al., 2009; ObSERVE, Rogan et al., 2018a), as well as smaller-scale abundance estimates for the resident populations in the Shannon Estuary and the west coast (Nykänen, Ingram, & Rogan, 2015; Rogan et al., 2018b), there has been no systematic attempt to model bottlenose dolphin seasonal habitat preferences over a large geographical scale.

The aim of this study was to investigate the habitat use of pelagic bottlenose dolphins in the Irish EEZ using GAMs. Furthermore, we tested the hypothesis that these habitat use patterns may vary between shelf, slope, and abyssal waters. The predictive power of the best fitting models was assessed. Finally, we elucidated whether the number of dolphins sighted varies depending on the same environmental covariates that influence the likelihood of their presence in an area.

2.2. METHODS

2.2.1. Study area and survey design

The study area comprised most of Ireland’s EEZ in the northeast Atlantic. This region covers a range of habitat types, extending from shallow coastal waters to beyond the continental slope. The edge of the continental shelf is quite close to the coast in some areas, creating upwellings and currents, as does the presence of deep trenches such as the Rockall Trough in offshore waters (Huthnance, 1986).

Aerial line-transect surveys were conducted in this area as part of Ireland’s ObSERVE Programme to assess marine megafauna presence and abundance in Irish waters. The study area was divided into eight strata and, within each stratum, two survey transects were randomly generated that would allow equal coverage probability and minimise design-based bias in the spatial distribution of aerial transect coverage. Surveys were flown

along these tracklines, using a high-wing twin-engine Britten Norman Islander fitted with bubble windows, giving observers unrestricted views of the area underneath the aircraft. Surveys were flown at 90 kn, at a height of 183 m above sea level, in Beaufort sea state <4 whenever possible. Two trained observers continuously scanned the water on either side of the aircraft, from directly below out to 500 m, while two other individuals logged the data. These data included the GPS location, date and time of each sighting, species and group size of megafauna observed. Sighting conditions, including Beaufort sea state, cloud cover, and glare, were recorded at the start and endpoint of each trackline, or each time an observer considered that these conditions had changed. The plane's position was also automatically recorded every two seconds using an onboard GPS linked to a data logging computer.

The survey lines were flown in two seasons for each of two survey years, Summer 1 (June–July 2015), Winter 1 (November 2015–February 2016), Summer 2 (May–July 2016), and Winter 2 (November 2016–March 2017) (Figure 2.1). The three inshore strata were only surveyed in the second year.

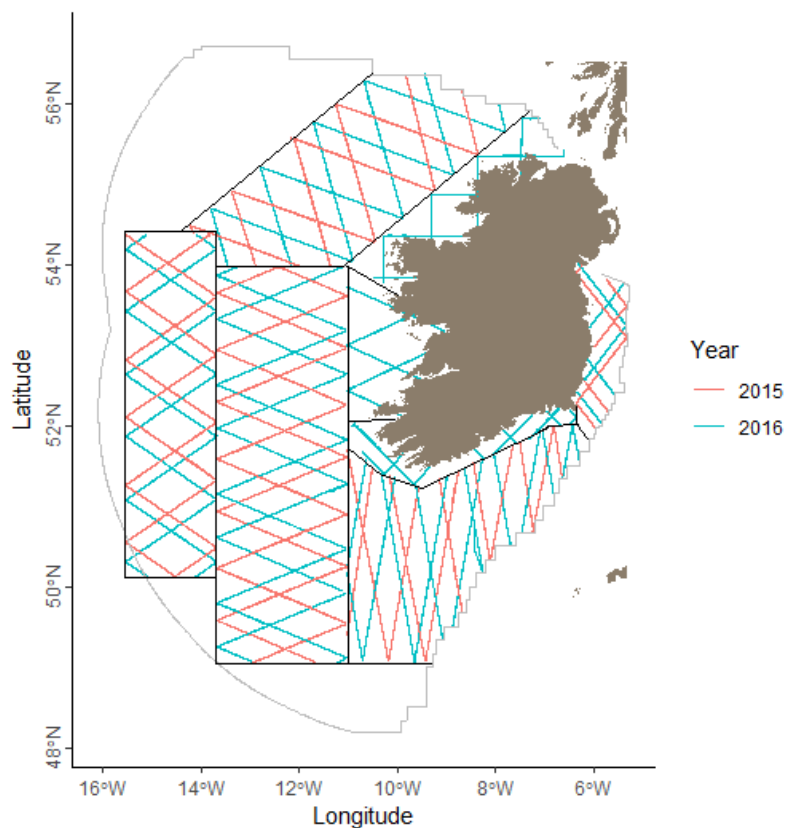


Figure 2.1. Map of aerial survey effort of the Irish EEZ (grey line) in each of two survey years of the ObSERVE programme, the first starting in 2015 and the second in 2016. Black lines indicate the division of the study area into eight strata.

2.2.2. Environmental data

Static and dynamic environmental variables covering the entire survey area, at a spatial grid resolution of 0.1 x 0.1 decimal degrees, were obtained from a variety of sources (Table 2.1). Static variables included depth, slope, seabed rugosity (the standard deviation of depth within a given area), and seabed aspect, all of which can affect prey distribution (Ferrari et al 2017; McArthur et al 2010) and bottlenose dolphin foraging tactics (e.g., Torres & Read 2009). Distance from the coastline (Forney et al., 2015) and from various depth contours was also included. Dynamic habitat predictors included sea surface temperature (SST), chlorophyll *a* concentration (chl), mixed layer depth, and sea bottom temperature, all of which are proxies for potential prey distribution. Finally, the standard deviations of both SST and chl were used as proxies for the presence of fronts (Forney et al., 2015), with which marine top predators, including bottlenose dolphins, are often associated (Scales et al., 2014; Cox et al., 2018).

The presence of multicollinearity among explanatory variables was assessed for each season separately using the Variance Inflation Factor (VIF). Starting with the entire suite of covariates, their VIFs were calculated and the variables with the highest values were sequentially dropped until all the remaining ones had a VIF <5. The remaining variables were also visually assessed for correlation using pairwise scatterplots.

Table 2.1. Environmental covariates used in the habitat preference modelling of bottlenose dolphins in Irish waters, shown with their abbreviations in the text, the calculation method for each cell, and the data source. (Continued on following page)

Variable	Name in text	Value for each grid cell	Source
Static			
Depth	depth	Average depth (m)	2-Minute Gridded Global Relief Data (ETOPO2v2). National Geophysical Data Center (NGDC). NOAA Satellite and Information Service.
Slope	slope	Maximum rate of change in value from that cell to its 8 neighbouring cells (degrees)	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
Seabed rugosity	rugosity	Standard deviation of depth within the cell	Calculated with R's 'raster' package from the depth data
Distance from land	dist0	Distance of the cell's centre to the 0 m depth contour (decimal degrees)	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.
Distance from the 1000 m depth contour	dist1000	Distance of the cell's centre to the 1000 m depth contour (decimal degrees)	Calculated with the Spatial Analyst extension of ArcGis 9.2, using GEBCO bathymetric data.

Distance from the 2000 m depth contour	dist2000	Distance of the cell's centre to the 2000 m depth contour (decimal degrees)	Calculated with the Spatial Analyst extension of ArcGIS 9.2, using GEBCO bathymetric data.
Seabed aspect	aspect	Average compass direction (degrees) the seabed faces	Calculated with the Spatial Analyst extension of ArcGIS 9.2, using GEBCO bathymetric data.
Habitat classifier	"Habitat"	Predominant characterisation within the cell as "Abyss", "slope", or "Shelf"	Calculated based on depth values: Abyss >1500 m, Shelf <800 m, slope between 800–1500 m
Dynamic			
Sea surface temperature	SST	Average SST (°C) for each of the four survey seasons	Sensor: Moderate Resolution Imaging Spectroradiometer (MODIS) on Aqua, Advanced Very High Resolution Radiometer (AVHRR) on POES, Imager on GOES, Advanced Microwave Scanning Radiometer (AMSR-E) on Aqua. Resolution: 0.1 degrees. NOAA CoastWatch Program
Sea bottom temperature	SBT	Average SBT (°C) for each of the four survey seasons	Sensor: Moderate Resolution Imaging Spectroradiometer (MODIS) on Aqua, Advanced Very High Resolution Radiometer (AVHRR) on POES, Imager on GOES, Advanced Microwave Scanning Radiometer (AMSR-E) on Aqua. Resolution: 0.1 degrees. NOAA CoastWatch Program
Chlorophyll <i>a</i>	chl	Average chlorophyll <i>a</i> concentration (mg m ⁻³)	Chlorophyll <i>a</i> (mg/m ³) was available from the NEO NASA website as a floating point GeoTIFF. Resolution 0.1 degrees.
Mixed layer depth	MLD	Modelled means of the 15 th of each month, averaged for each of the four survey periods	Downloaded from the Marine Institute Data Portal (http://data.marine.ie/). Resolution was available as 0.025dd grid squares and scaled up to 0.1dd
Sea surface temperature SD	SST fronts	Standard deviation of SST in the five nearest grid cells	Calculated with R's 'raster' package from the SST data
Chlorophyll <i>a</i> SD	chl fronts	Standard deviation of chl in the five nearest grid cells	Calculated with R's 'raster' package from the chl data

2.2.3. Model setup and selection

The distribution of bottlenose dolphins was examined using a number of approaches, using the package 'mgcv' (Wood, 2003, 2011) in R version 3.5.0 (R Core Team 2018).

To investigate habitat use at the level of the entire study area, we ran binomial GAMs with a logit link function, using the presence/absence of dolphins in each grid cell as a response variable, and the environmental variables as predictors. Each cell was assigned a value of

1 if one or more bottlenose dolphin sightings occurred in it, or 0 if no sightings were recorded in it.

Further, to assess how bottlenose dolphin habitat use differed between the shelf, slope, and abyssal waters in the study area, each grid cell was assigned a factor variable, “Habitat”, depending on which of those three locations it occupied. This factor was added as an interaction term to some of the predictor variables in the previous models. Specifically, the “Habitat” interaction term was added to the rugosity smooth and all dynamic covariates. We considered it superfluous to add it to the depth covariate, as depth is the main feature that the shelf/slope/abyss categories are based on; similarly, including the interaction with the distance covariates made the models over-fit.

To investigate whether the number of dolphins per cell was influenced by the environment, we ran GAMs using the count of dolphins in each grid cell where they were observed as a response variable, with the same suite of environmental covariates used in the binomial GAMs for each season. As the data were overdispersed, a quasi-likelihood approach with Poisson-like assumptions (quasi-Poisson) was used instead of a simple Poisson distribution, and cells with no dolphin sightings were excluded from the dataset (i.e., count data were modelled conditional on presence).

To test the best models’ descriptive and predictive power, one set of summer and winter observations was used as a training dataset and the other as a test dataset. Because the surveys in the last two seasons were more comprehensive (covering inshore strata), Summer 2 and Winter 2 were selected to train the models, which were then tested with the data from Summer 1 and Winter 1. The values of each predictor variable were standardised around the mean and standard deviation; for the dynamic covariates, this was computed separately for each season. Specifically, for each standardised value, we subtracted the mean of that variable from each non-standardised observation, and divided the result by the standard deviation of that variable. To avoid information leakage (i.e., using information from outside the range of values used to fit the initial models), the covariate values of the test dataset (Summer 1 and Winter 1) were standardised around the means and standard deviations of the training dataset.

We assessed the ability of the binomial GAMs to describe the ecological processes that determine bottlenose dolphin distribution by using the best fitting models resulting from the model selection procedure to predict bottlenose dolphin occurrence in the training

dataset. That is, the best model for each of the last two survey seasons was used to predict the probability of presence of dolphins in each cell given the corresponding values of the environmental covariates in those seasons. A receiver operating characteristic (ROC) curve was drawn for each set of predictions and used to calculate a threshold over which the predicted probability was converted to a presence and below which it was converted to an absence. These reassigned values were then placed in a confusion matrix with the actual observations to compare predicted versus observed values. The percentage of correctly predicted presences and absences were calculated as an indicator of model goodness-of-fit, i.e., the higher the percentage of correct predictions, the better the model's performance in describing observed habitat use.

We tested the binomial models' predictive capacity by making them retrodict (predict backwards) the probability of dolphin occurrence in the first two survey seasons. Using the same threshold calculated for the training dataset as a cut-off point to convert probabilities to presences and absences, the predicted and observed values were placed in a confusion matrix and the percentage of correctly assigned values was calculated as an indicator of the model's predictive strength.

Each season of the training dataset was modelled separately, starting with all the non-collinear variables for that season. With the exception of aspect, we used a thin-plate regression spline for each of the environmental predictors, allowing the effective degrees of freedom to shrink to zero if a variable did not inform model fit in any way. As aspect is a cyclical variable, meaning the lowest value is equal to the highest ($0^\circ=360^\circ$), a cyclical spline was used for its smooth. Terms shrunk to zero and non-significant terms were dropped from the model until only significant predictors remained (Redfern et al., 2017). Model fit was assessed based on the deviance explained by each.

Residual autocorrelation was assessed using an autocorrelation function (ACF) plot. Because there was an indication of autocorrelation between neighbouring residuals, the range of this autocorrelation was investigated using a spherical spatial correlation structure fitted in mixed effect GAMs (GAMMs), with latitude and longitude coordinates included as a random effect. The estimated range proved to be just under the width of two grid cells, confirming that autocorrelation was low. To account for it, a two-dimensional random effect spline of latitude and longitude was included in the models.

An effort variable was also included in all models to account for variation in survey effort between grid cells. A half-normal detection function was used to determine effective strip width for each grid cell. For dolphins, this can be affected by Beaufort sea state, so each grid cell was assigned an effective strip width depending on the prevailing sea state in which that cell was surveyed. The effort metric for each cell was calculated as the length L of the transect segment crossing the cell, multiplied by twice the effective strip width ESW for that cell (or $L*2*ESW$).

2.3. RESULTS

2.3.1. Surveys

In the first survey year, 16,797 km of survey effort were flown, while in the second year, with the added inshore strata, 20,387 km were surveyed. A total of 640 bottlenose dolphin sightings were recorded, 102 in the first year and 435 in the second. Dolphins were sighted in all surveyed strata (Figure 2.2); however, because there was only one sighting in the Irish Sea in 2016, that stratum was excluded from all further analyses. The lowest number of sightings was recorded in the first Summer season, while the highest was observed in the second Winter season (Table 2.2). The resulting abundance estimates from the ObSERVE report (Rogan et al., 2018) are shown in Appendix IA. Both Winter seasons had more dolphin sightings than their preceding Summer seasons, while the latter year had more sightings than the first, even allowing for the additional inshore strata surveyed. A large number of dolphin groups were encountered close to the southwest coastline in Summer 2. Average group size varied between seasons, from 4 animals in the first winter to 8 in the second. The largest group recorded was of 120 individuals sighted in an offshore stratum northwest of Donegal (Figure 2.2) in Winter 2. Overall, the sightings appeared to be evenly dispersed across all strata except for the Irish Sea and the waters north of Ireland, and apart from the first Summer season.

Table 2.2. Number of bottlenose dolphin sightings in offshore and inshore strata and mean (min–max) group size recorded in each of the four survey seasons (from Rogan et al., 2018a).

	Summer 1	Winter 1	Summer 2	Winter 2
Sightings				
<i>Offshore strata</i>	18	84	102	251
<i>Inshore strata</i>	NA	NA	59	23
Total	18	84	161	274
Group size				
	6.74 (1–25)	4.33 (1–27)	7.12 (1–45)	8.21 (1–120)

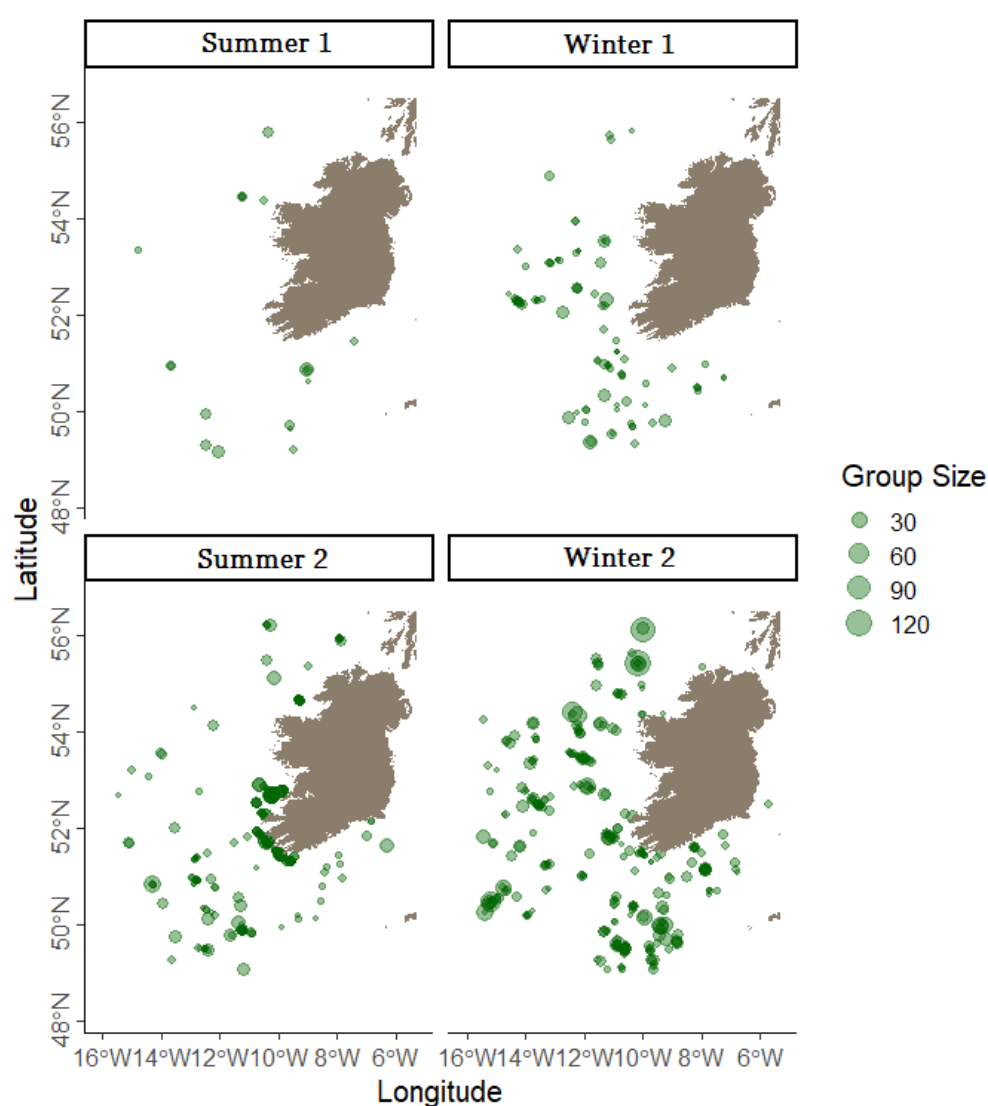


Figure 2.2. Bottlenose dolphin sightings from aerial surveys in Irish waters in each of four seasons (Summer 1 and Winter 1 commencing in 2015, Summer 2 and Winter 2 commencing in 2016). Circle diameter reflects group size. Overlapping circles denote multiple sightings that were close together.

2.3.2. Model covariates and results

The covariates retained in the models varied throughout the study area and between seasons. Maximum depth was 4817 m, with a mean value of 885 m. Seabed rugosity was highest near the continental slope. Mixed layer depth (MLD) in summer was shallower than in winter (mean values of 36 m and 190 m, respectively). Sea surface temperature (SST) ranged from 7–13°C in winter and 11–17°C in summer, while sea bottom temperature (SBT) ranged between 2–12°C and 2–15°C in each season. Average chlorophyll a (chl) values were 0.7 mg m⁻³ and 0.9 mg m⁻³ in winter and summer, with highest concentrations of 26 mg m⁻³ and 12 mg m⁻³, respectively.

The initial binomial models and the explanatory variables retained in the final ones are shown in Table 2.3. Due to high collinearity with other variables (VIF>5), the following variables were excluded from some initial models: slope was excluded from all models, depth was excluded from the winter models, aspect was excluded from the winter model sans “Habitat” interaction, SBT was excluded from the summer models, and distance from the one and two thousand metre depth contours (dist1000 and dist2000) were excluded from the summer and winter models, respectively. All the binomial models explained >20% of the observed deviance, with neither of the seasonally explicit models performing consistently better based on the deviance explained. The inclusion of the habitat classifier did not consistently improve performance; the winter model performed better than the summer one when the interaction was not included, but the summer model performed better than the winter one when the interaction was included. The inclusion of the interaction term improved model fit for the summer season, but not for the winter season.

Table 2.3. Variables included in the starting models, significant covariates retained in each model denoted by *, and percentage of the deviance explained by each model as a measure of its performance. (For explanation of abbreviations, see Table 2.1).

Model	Model covariates	% deviance explained
Binomial without interaction term		
Summer 2	SST, MLD*, chl, SST fronts*, chl fronts, depth*, rugosity, dist0*, dist2000, aspect*	22.9
Winter 2	SST*, MLD, chl, SST fronts, chl fronts, SBT*, rugosity*, dist0*, dist1000*	23.5
Binomial with interaction term		
Summer 2	SST:'Habitat'*, MLD:'Habitat'*, chl:'Habitat'*, SST fronts:'Habitat'*, chl fronts:'Habitat', depth, rugosity:'Habitat'*, dist0, aspect:'Habitat'*	32.4
Winter 2	SST:'Habitat'*, MLD:'Habitat'*, chl:'Habitat', SST fronts:'Habitat', chl fronts:'Habitat'*, SBT:'Habitat'*, rugosity:'Habitat', dist0*, dist1000, aspect:'Habitat'	22.1

2.3.3. Relationship between dolphin presence and environmental covariates

The presence of dolphins in summer was negatively correlated with MLD and overall positively correlated with SST fronts, although that smooth showed considerable wiggleness, indicative of potential over-fitting. Dolphin occurrence peaked at several depths, at approximately 1000, 2000, and >4000 m, while, in relation to seabed aspect, it decreased between 50° and 160° (or on northeast- and south-southeast-facing slopes). Dolphin presence peaked at 50 km and then again at approximately 170 km from the coastline, showing decreasing association with more offshore waters (Figure 2.3).

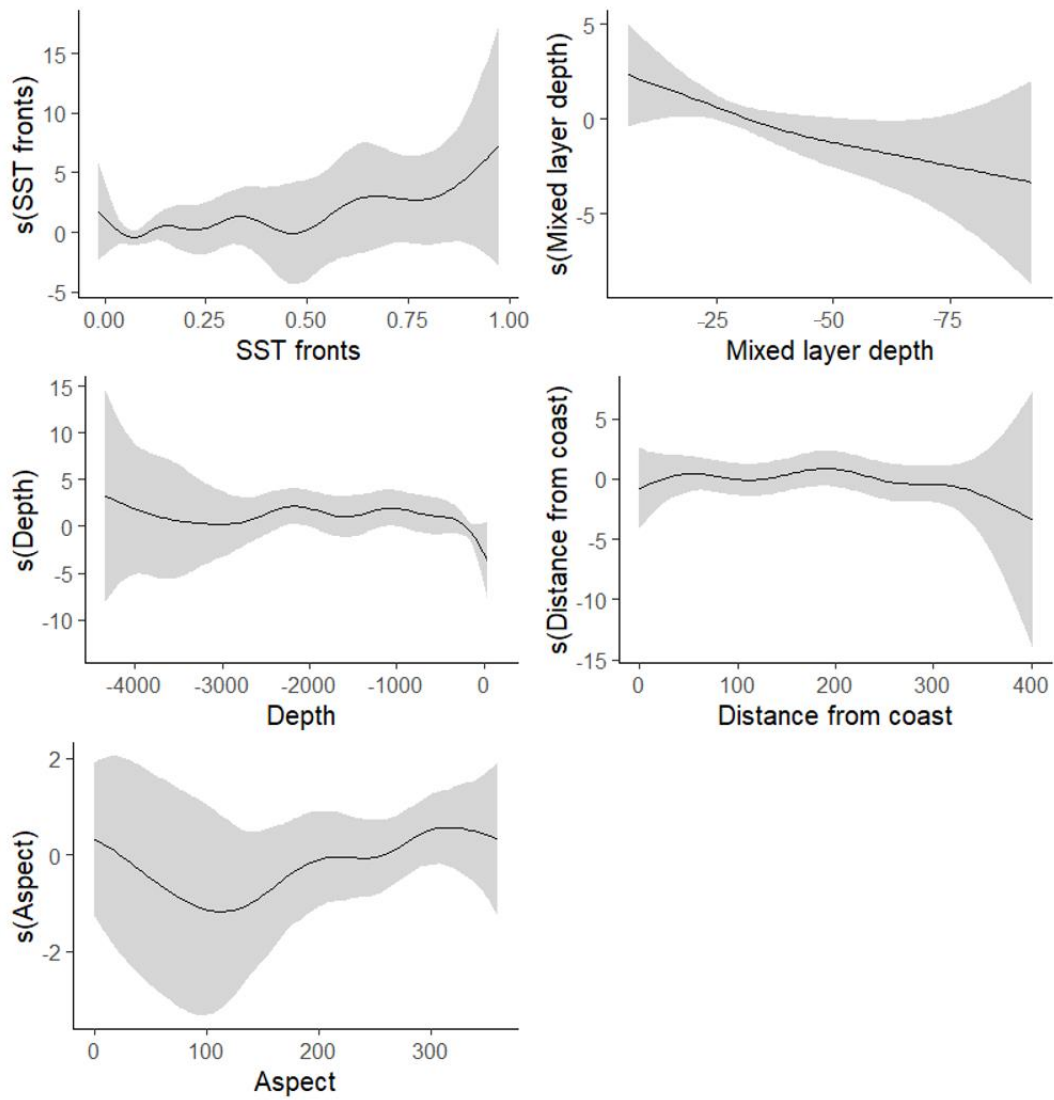


Figure 2.3. Estimated smoothing curves of the relationship between the presence of dolphins and significant environmental variables for binomial models of Summer 2 (May–July 2016). Solid lines are the smoothers and shaded regions indicate 95% confidence intervals. Y-axis shows strength of the effect of each covariate on dolphin presence.

In winter, bottlenose dolphins appeared to associate less with low or high surface temperatures, peaking at intermediate temperatures of approximately 11°C, while their presence increased at lower (5°C) and high (10–12°C) bottom temperatures. They also showed a preference for substrates of medium or high rugosity and areas very close to (<50 km) or very far from (>250 km) the coastline and appeared to avoid areas far (>300 km) from the 1000 m depth contour (Figure 2.4).

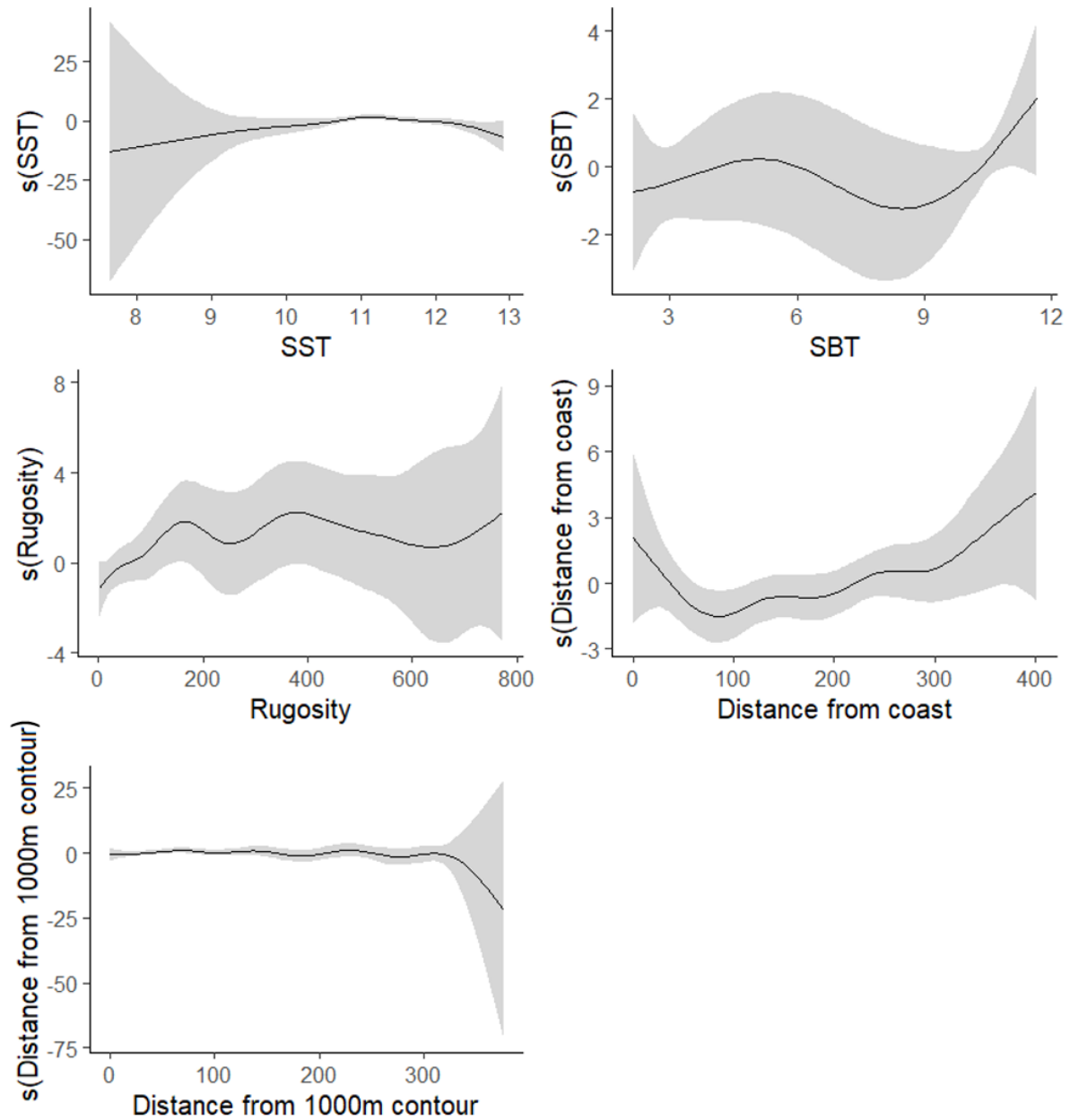


Figure 2.4. Estimated smoothing curves of the relationship between the presence of dolphins and significant environmental variables for binomial models of Winter 2 (November 2016–February 2017). Solid lines are the smoothers and shaded regions indicate 95% confidence intervals. Y-axis shows strength of the effect of each covariate on dolphin presence.

2.3.4. Including habitat classification in binomial models

Dolphin presence in Summer showed a significant positive correlation with SST in abyssal habitats, and a significant negative correlation with MLD in shelf and slope waters; furthermore, there is a significant negative correlation with chl and SST fronts on the continental slope, but an overall positive correlation with SST fronts on the continental

shelf, although the wiggleness of that smooth is indicative of over-fitting. Seabed rugosity showed a negative effect on dolphin presence in abyssal waters, while seabed aspect significantly affected dolphin occurrence along the continental slope (Figure 2.5).

In Winter, SST was significant in shelf waters, with dolphin occurrence peaking at medium temperatures rather than the extremes; MLD showed a significant positive effect on dolphin presence in slope waters, while chl fronts had similar positive effects in both slope and abyssal habitats. SBT had a positive effect on dolphin presence on the continental shelf, but a non-linear relationship with it along the continental slope, with dolphin presence decreasing around the mean bottom temperatures and increasing again with higher temperatures. Dolphins presence was higher in areas close to the coastline, increasing again very slightly before decreasing again at furthest distances from shore (Figure 2.6).

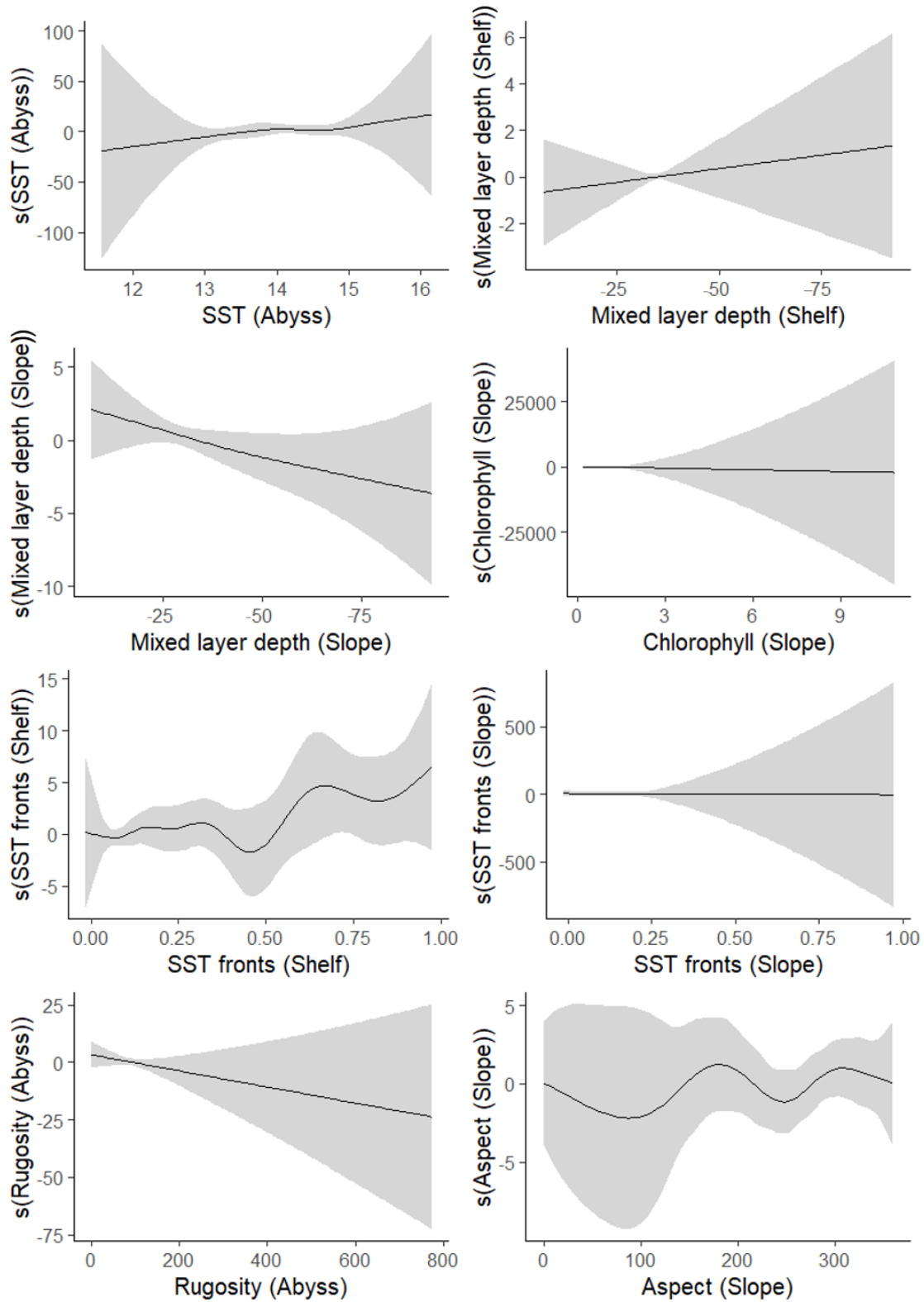


Figure 2.5. Estimated smoothing curves of the relationship between the presence of dolphins and significant environmental variables for binomial models of Summer 2 (May–July 2016) when a habitat interaction term was included. Term in brackets indicates which habitat region (continental shelf, continental slope, or abyss) the smoother relates to. Solid lines are the smoothers and shaded regions indicate 95% confidence intervals. Y-axis shows strength of the effect of each covariate on dolphin presence.

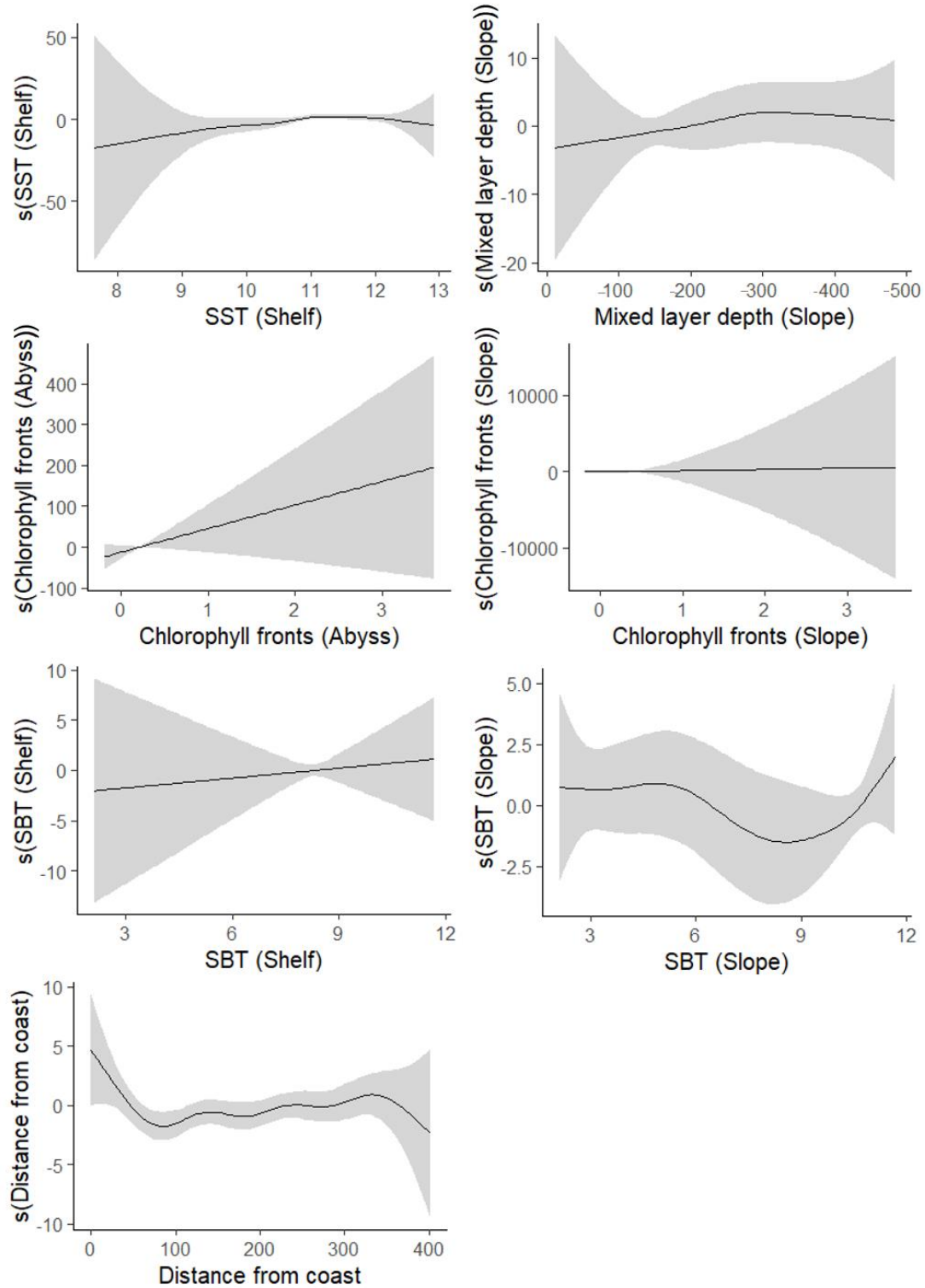


Figure 2.6. Estimated smoothing curves of the relationship between the presence of dolphins and significant environmental variables for binomial models of Winter 2 (November 2016–February 2017) when a habitat interaction term was included. Term in brackets indicates which habitat region (continental shelf, continental slope, or abyss) the smoother relates to. Solid lines are the smoothers and shaded regions indicate 95% confidence intervals. Y-axis shows strength of the effect of each covariate on dolphin presence.

2.3.5. Number of dolphins per cell

The environmental variables included in the initial models of the number of dolphins per cell and retained after covariate selection are shown in Table 2.4. Slope was again excluded due to high collinearity, as was dist1000 from the summer model and dist2000 from the winter model. Dist1000 was also excluded from the summer model because the lower number of observations did not allow the model to converge when including that many parameters. In summer, chl was the only variable with a linear negative effect on the number of dolphins observed (although that trend is driven by very few sightings in high chl concentrations, hence the large margin of error), while MLD showed an overall positive effect on dolphin numbers. SST fronts and chl fronts showed opposite effects on the number of dolphins observed, with lower numbers of dolphins occurring in areas of high or low SST variability and higher ones occurring in areas of high or low chl variability (Figure 2.7).

Table 2.4. Variables included in the initial quasi-Poisson models, significant covariates retained in each model denoted by *, and percentage of the deviance explained by each model as a measure of its performance. (For explanation of abbreviations, see Table 2.1).

Season	Model covariates	Deviance explained
Summer 2	SST, MLD*, chl*, SST fronts*, chl fronts*, depth, rugosity, dist0, aspect	71.5%
Winter 2	SST, MLD*, chl, SST fronts, chl fronts, SBT, rugosity*, dist0*, dist1000, aspect*	45.4%

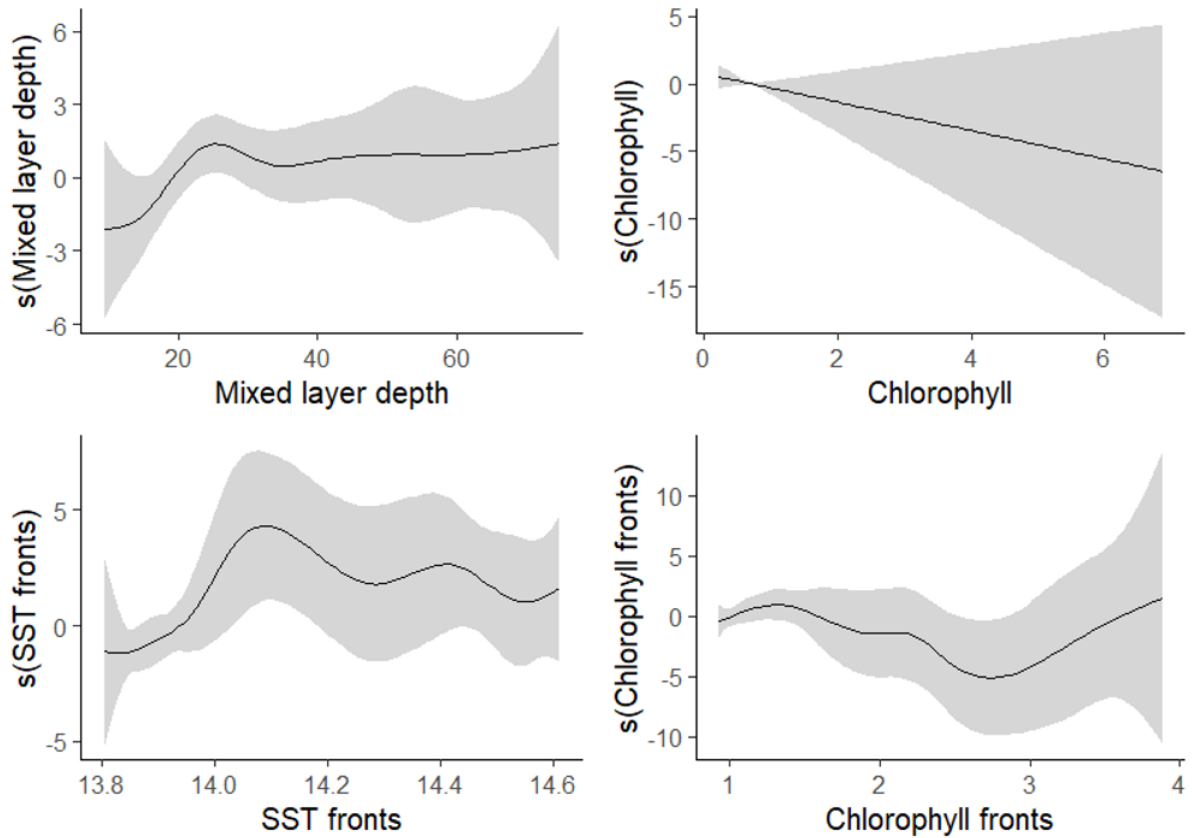


Figure 2.7. Estimated smoothing curves of the relationship between the number of dolphins per grid cell and significant environmental variables for quasi-Poisson models of Summer 2 (May–July 2016). Solid lines are the smoothers and shaded regions indicate 95% confidence intervals. Y-axis shows strength of the effect of each covariate on dolphin presence.

In winter, MLD correlated positively with the number of dolphins, whereas rugosity did not show a clear pattern. Dolphin numbers peaked several times in relation to distance from shore but increased primarily at furthest distances (>300 km from land). The largest aggregations of dolphins were observed in aspects between 180° and 280° (or between south- to west-facing slopes) (Figure 2.8).

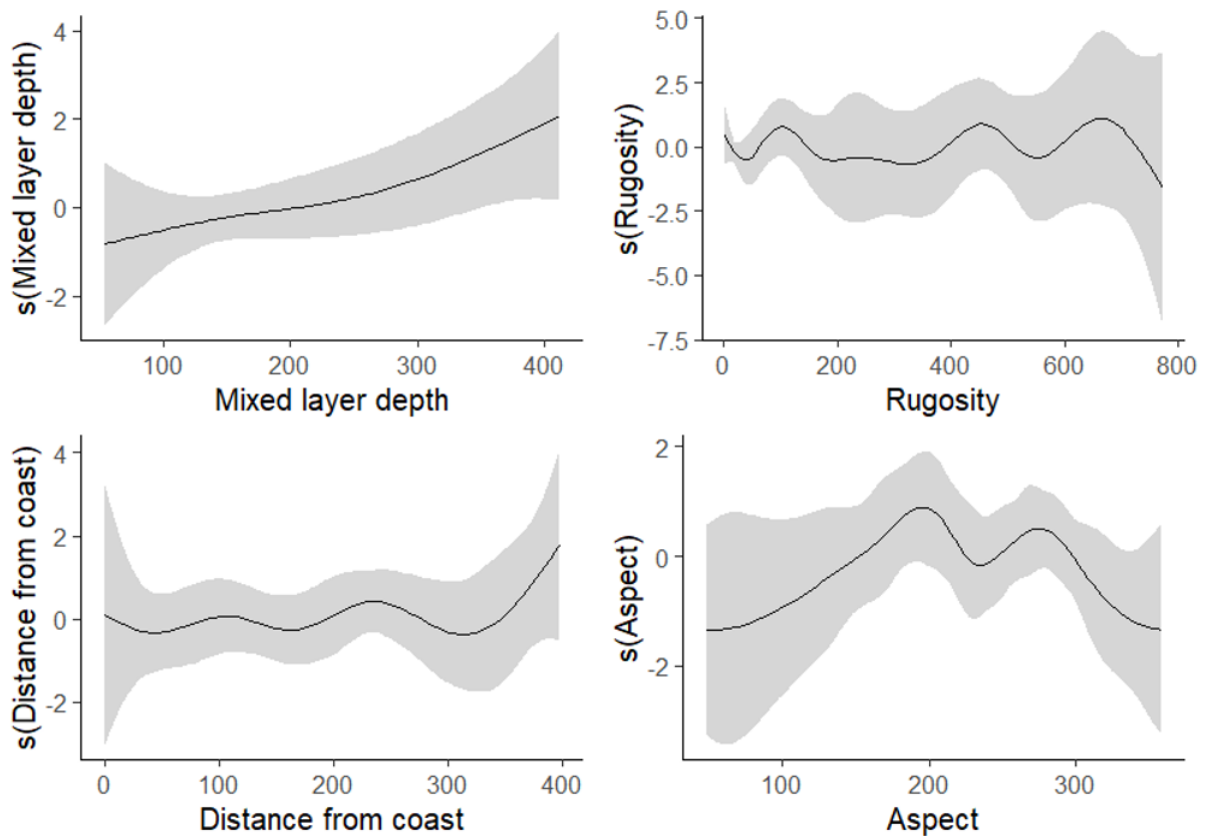


Figure 2.8. Estimated smoothing curves of the relationship between the number of dolphins per grid cell and significant environmental variables for quasi-Poisson models of Winter 2 (November 2016–February 2017). Solid lines are the smoothers and shaded regions indicate 95% confidence intervals. Y-axis shows strength of the effect of each covariate on dolphin presence.

2.3.6. Assessing the models' descriptive power

When the best fitting models for each of the training seasons were used to predict dolphin occurrence based on the same environmental covariates, they performed well (both presences and absences correctly predicted >69% of the time; Table 2.5), indicating good descriptive power within each survey period. Including the 'Habitat' interaction term improved the model's overall descriptive power in Summer, but not in Winter. The predicted sighting probabilities are mapped in Figure 2.9, and their associated confidence intervals are given in Appendix IB (Figure IB.1).

Table 2.5. Percentage of bottlenose dolphin presences and absences predicted correctly for the last two survey seasons by binomial models trained on observations in those two seasons. “Interaction” refers to the inclusion of a factor interaction with the ‘Habitat’ classifier.

Model	Presences predicted correctly	Absences predicted correctly	Average % of correct predictions
Summer 2			
GAM with no interaction	74.46%	76.58%	75.52%
GAM with interaction	73.40%	84.00%	78.70%
Winter 2			
GAM with no interaction	77.57%	76.80%	77.18%
GAM with interaction	81.70%	69.93%	75.81%

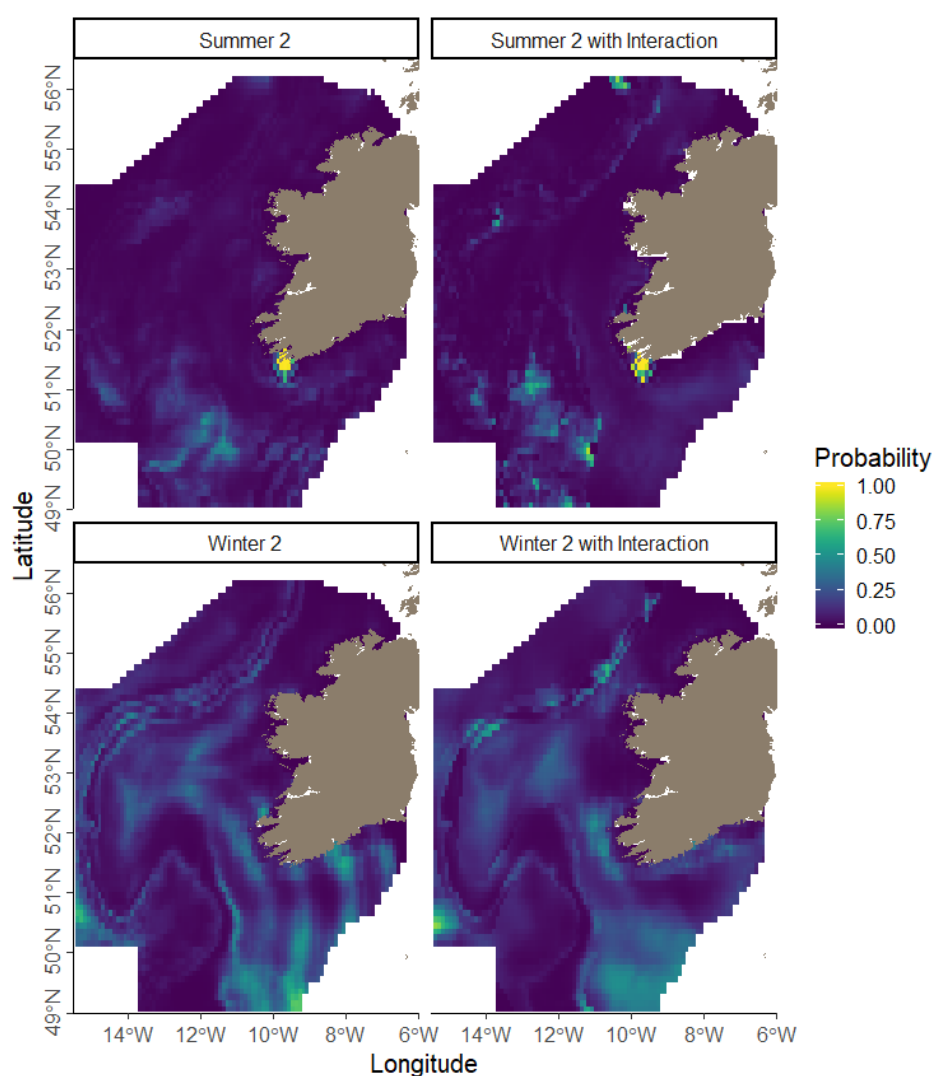


Figure 2.9. Predicted sighting probabilities for Summer 2 (1st row), Winter 2 (2nd row), using binomial GAMS not including the ‘Habitat’ interaction term (1st column) and including it (2nd column). For associated 95% confidence intervals see Appendix IB.

2.3.7. Assessing the models' predictive capacity

When the best fitting models for each of the training seasons were used to predict dolphin occurrence in 2015 based on the test covariates (the first two seasons), they performed less consistently than when predicting their concomitant sightings (varying in accuracy from 28.57% to 78.85% correct predictions; Table 2.6). As with their descriptive capacity, including the 'Habitat' interaction term improved the model's predictive power in Summer but not in Winter. The predicted sighting probabilities for each season and model are mapped in Figure 2.10 and their associated confidence intervals are given in Appendix IB (Figure IB.2).

Table 2.6. Percentage of bottlenose dolphin presences and absences predicted correctly for the first two survey seasons by binomial models trained on observations in the last two seasons. "Interaction" refers to the inclusion of a factor interaction with the habitat 'Habitat' classifier.

Model	Presences predicted correctly	Absences predicted correctly	Average % of correct predictions
Summer 2015			
GAM with no interaction	57.14%	48.55%	52.84%
GAM with interaction	28.57%	78.85%	53.71%
Winter 2015			
GAM with no interaction	57.37%	68.68%	63.02%
GAM with interaction	63.33%	43.29%	53.31%

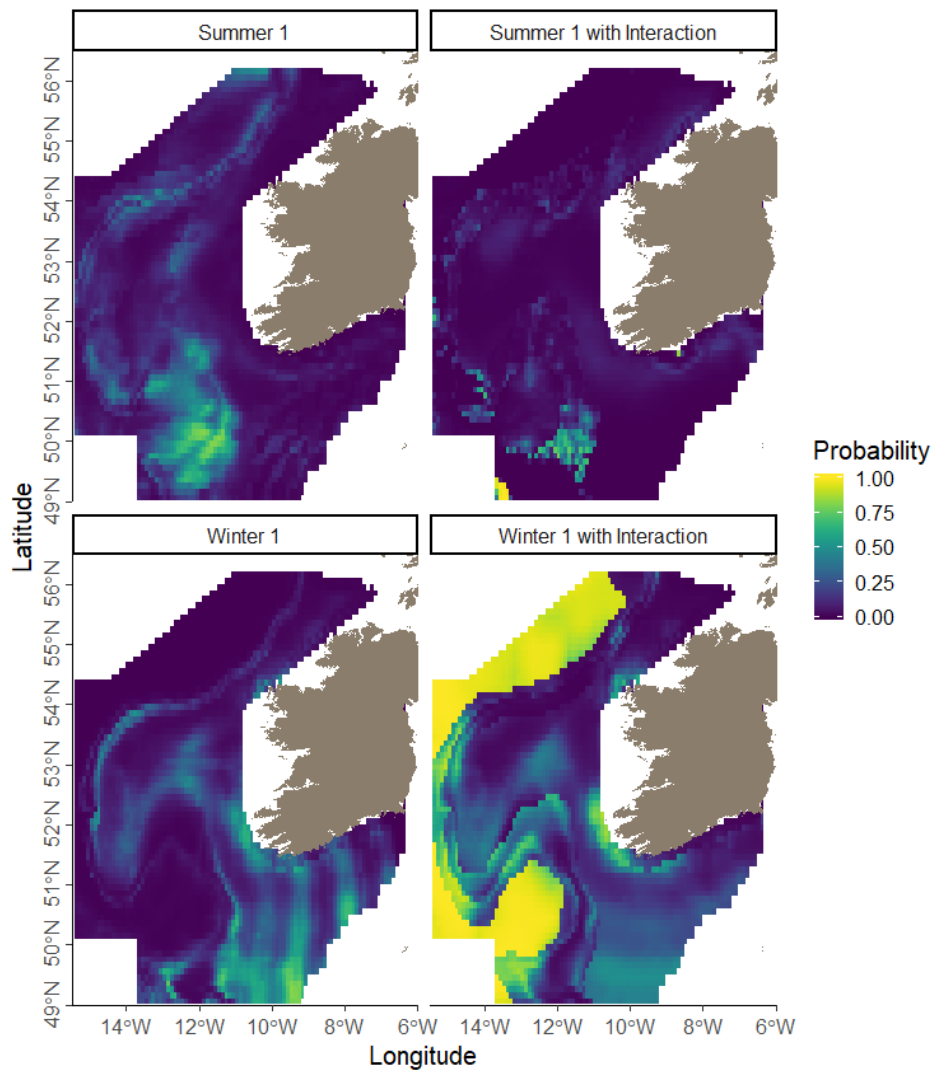


Figure 2.10. Predicted sighting probabilities for Summer 1 (1st row) and Winter 1 (2nd row), using binomial GAMs trained on the Summer 2 and Winter 2 observations. 1st column: models excluding an interaction with 'Habitat'; 2nd column: interaction with 'Habitat' included. For associated 95% confidence intervals of predictions see Appendix IB.

2.4. DISCUSSION

Several attempts have been made to estimate the abundance and distribution of odontocetes in the Northeast Atlantic, both at small, regional scales (Shannon Estuary, west coast of Ireland, west coast of Scotland) and on larger scales, as part of multi-species surveys (e.g., SCANS I–III, CODA, ObSERVE), but this study is the first to examine in detail the seasonal habitat use of bottlenose dolphins over most of the Irish EEZ. Although some bottlenose dolphin populations in Irish waters show considerable site fidelity and appear socially and genetically distinct from other populations (Mirimin et al., 2011, Louis et al., 2014a, Oudejans et al., 2015), there have been observations of long-distance movements around the Irish coastline (e.g. Nykänen et al. 2018) and further afield

(O'Brien et al., 2009; Robinson et al., 2012). This makes it difficult to determine the habitat preferences and spatial distribution of these different populations, impeding the designation of protected areas and the development of adequate conservation and marine spatial planning schemes.

Using aerial survey data of the Irish Atlantic margin, we were able to model dolphin distribution on a scale encompassing some of these long-distance movements and elucidate the habitat preferences of bottlenose dolphins in this region. We did this using progressively more complex models: first, we investigated how dolphin presence varied with environmental features over the entire region, then we assessed whether the importance of these variables was consistent in different parts of the marine environment, and, finally, we evaluated whether the size of dolphin aggregations was affected by the same environmental drivers as dolphin presence. We also tested the ability of the models to predict dolphin distribution both within the seasons on which they were trained (i.e., their goodness-of-fit) and for seasons outside the training dataset.

2.4.1. Importance of environmental predictors

The variables retained in each model led to reasonably good model fit, with >20% of deviance explained in every case, considering that most of the environmental covariates used in the models are proxies for prey distribution, and that bottlenose dolphins may show high plasticity in habitat use and diet (Bonizzoni et al., 2013; Hartel, Constantine, & Torres, 2015; Milmann et al., 2016). The flexibility of GAMs is important for capturing the complexities of the animals' relationship with their environment. Different variables were retained as significant in each model, with MLD and dist0 being the most ubiquitous (significant in all but two models) and depth and dist1000 only informing one model each (the no-interaction binomial summer and winter model, respectively). MLD had a negative effect on the presence of dolphins in all but slope waters in winter, where its effect was positive. Its effect was also positive on the number of dolphins sighted in both seasons (i.e., more dolphins associated with deeper mixed layers). A greater mixed layer depth when primary productivity is generally low (both in winter and summer) could increase plankton production through the cycling of deeper nutrients (Polovina, Mitchum, & Evans, 1995). This increased productivity likely attracts animals that dolphins can feed on, and larger aggregations of prey may explain the higher numbers of dolphins seen in areas with deeper mixed layers. It is unclear why MLD appears to negatively influence the probability

of sighting dolphins in shelf and abyssal waters in winter, but its effect is possibly compounded by other factors that influence prey distribution.

Dolphin presence was associated with medium to high surface temperatures in winter, specifically in abyssal waters, and in shelf waters during the summer, which could be due to physiological constraints on the animals themselves or on their prey species. In cells where dolphins were sighted, i.e., in milder waters, dolphin numbers were not significantly correlated with surface temperature. Although warmer surface temperatures are associated with more stratified waters and less nutrient mixing, they may be beneficial for the growth and recruitment of larval stages of some fish and cephalopod species (Otterlei et al., 1999; Bellido, Pierce, & Wang, 2001; Pörtner et al., 2001; van der Kooij, Engelhard, & Righton, 2016), thus affecting dolphin prey availability. SST fronts also had a positive influence on dolphin presence during the summer, and were significant in predicting summer numbers, as well, although dolphin numbers peaked at medium values of variability. Higher variability in surface temperatures is associated with water mixing and nutrient upwellings, which are known to attract marine megafauna (Jonker & Bester, 1998; Gannier & Praca, 2007; Weimerskirch, 2007; Petersen et al., 2008; Bost et al., 2009; Scales et al., 2014). That the relationship between thermal fronts and dolphin numbers was not linear could be a result of the interplay with other environmental factors or over-fitting.

In winter, SBT had a non-linear relationship with dolphin presence in the simple GAM and in slope waters when including the habitat classifier, as well as a directly positive influence in shelf waters. This likely reflects how benthic communities are affected by bottom temperatures, leading to higher or more diverse prey concentrations; the abundance of some cephalopod species, for instance, increases proportionately to SBT (Pierce et al., 2008). Although most studies on bottlenose dolphin diving behaviour have been restricted to near-shore populations, offshore individuals have been recorded diving to depths greater than 450 m (Klatsky, Wells, & Sweeney, 2007). Such deep dives would enable them to feed on demersal species in shelf waters, but not in abyssal areas (where the seabed is >1500 m from the surface), so it follows that any SBT changes in those areas would not have a direct effect on dolphin presence. While it is known that bottlenose dolphins have a range of different foraging techniques adapted to their various environments, details on their fine-scale dietary preferences in this region are lacking

(Rogan et al., 2011; Hernandez-Millian et al., 2015) and need to be further investigated before the mechanism that links SBT to dolphin occurrence can be understood.

Dolphin presence was affected by seabed aspect overall in the summer, though including the 'Habitat' interaction indicated that this relationship was driven primarily by sightings in slope waters, as the shape of the smooth functions is similar and only significant on that level. Aspect seemed to have the opposite influence on dolphin numbers during the winter. The aspect of slopes likely affects the way currents and upwellings are formed, influencing productivity. The direction and strength of currents can also influence the movements of potential prey species, such as cephalopods (Pierce et al. 2008). In winter, seabed rugosity had practically the inverse influence on dolphin presence and dolphin numbers, and a directly negative influence on dolphin presence in abyssal waters in the summer. Higher rugosity increases habitat complexity and is associated with more diverse benthic communities, which could be attractive to foraging dolphins; however, this relationship is clearly not directly linear in terms of dolphin numbers and has a negative effect on dolphin presence in abyssal waters. Ferrari et al. (2018) found that the abundance of some fish species is negatively correlated with rugosity, while others are positively affected. The significance of rugosity on only one 'Habitat' level could be an indication that dolphins feed on different prey species in the different habitat categories, some of which are affected by seabed topography and others of which are driven by more dynamic factors.

Bottlenose dolphins were observed more in coastal waters in the winter, in terms of both predicted likelihood of sightings and the predicted number of animals. The presence of dolphins was highest at distances within 50 km and beyond 300 km from shore, while higher numbers of dolphins per cell were observed at various distances from the coastline, namely within 20 km, at 100 km, 220 km, and beyond 350 km from the coast. When including the 'Habitat' factor interaction in the models, dolphin presence appeared to decrease at the furthest areas from shore, likely as a result of the shelf edge being quite close to the coast in some areas and considerably further in others. The estimated relationship with the 1000 m depth contour—i.e., dolphins avoiding areas further than 300 km from said contour—reflects the low number of sightings in the easternmost parts of the study area. While long-distance bottlenose dolphin movements between Irish and UK waters have been recorded (Robinson et al., 2012), the reason for their apparently low numbers in the Irish Sea and eastern Celtic Sea is not yet understood.

2.4.2. Spatial predictions and model performance

The predicted distribution of dolphin occurrence (Figures 2.9 and 2.10) showed that the continental shelf area is important in winter seasons, particularly to the south of Ireland. Higher probabilities of dolphin occurrence were also predicted along the continental slope in winter and in the first summer. In both summers, the Porcupine Basin (offshore) showed higher likelihood of dolphin presence, while in the second summer, the highest probability of occurrence was predicted to be on the southwest coast, where there is an upwelling feature (O'Boyle & Silke, 2010). These differences highlight the seasonality of bottlenose dolphin movements and the importance of investigating them on finer temporal scales, as dynamic environmental parameters can vary significantly between winter and summer. The increased presence of bottlenose dolphins across the shelf area in winter (and, indeed, their higher abundance estimates in the second winter) could reflect a seasonal move from further offshore, potentially following shifts in the distribution of prey, predator, or competitor species offshore. Each of these possibilities warrants further investigation, perhaps with the inclusion of multi-species distribution/abundance in similar habitat models.

By testing the models' predictive ability using the same data as those they were trained on, we assessed their power to describe the distribution of bottlenose dolphins within the survey area for that year. As shown by the high percentages of correctly predicted presences and absences, the best fitting models performed well in describing dolphin distribution patterns. However, when testing the models' predictive power on the previous year's data, they did not consistently perform as well. There are several reasons why this could be the case. First, aside from habitat characteristics that could physically and physiologically constrain animal movements, an important driver of habitat preferences is prey distribution (Hooker & Gerber, 2004; Carroll et al., 2017). For bottlenose dolphins in the Northeast Atlantic, not much is known about their diet (Rogan et al., 2011; Hernandez-Milian et al., 2015), and it is difficult to acquire abundance and distribution data on prey species. The predictor variables used in these habitat models are only proxies of prey distribution and do not fully capture the underlying processes that affect it. As a result, the models' ability to predict dolphin occurrence accurately outside the study period is reduced. Moreover, the year used as a test dataset, 2015, may have been particularly difficult to retrodict. It was an irregular year in terms of sea surface temperature, with some of the coldest monthly averages observed since 1948 (Duchez et al., 2016). This anomaly

will likely have affected species on all trophic levels, as well as exhibiting variable values (SST and chl, in particular) outside the range of values observed in the training dataset. The combination of statistical uncertainty in extrapolating to values outside the observed range and environmental irregularities could have contributed to the reduction of the models' ability to accurately predict dolphin occurrences in that year. While the models still managed to accurately retrodict sightings >50% of the time, inference about their overall performance is difficult because of the inconsistency in their predictive accuracy within and between seasons. Such inconsistencies reflect both the dolphins' plasticity in terms of habitat use and our own difficulty in modelling habitat preferences without detailed knowledge and data on the underlying drivers of their movement patterns. However, the present models are an important first step towards identifying potential environmental factors to further investigate, as well as highlighting gaps in our available data which need to be addressed.

This study is a first comprehensive investigation of bottlenose dolphin habitat distribution in Irish waters. No single environmental variable was a consistent predictor of either dolphin presence or numbers. In fact, even the most frequently retained covariates affected habitat selection differently depending on the seasonal context and the inclusion of other variables. This is a strong indication of the complexity of the factors determining the distribution of this top predator, showing that there is no single environmental characteristic, but rather an interplay of multiple variables driving habitat preferences. Moreover, not only were some variables only retained in the models when the 'Habitat' interaction was included, but the shape of the estimated relationships with certain covariates changed when that term was added. This highlights how the dolphins' habitat use changes as the habitat itself changes—again, both a reflection of their adaptive distribution patterns and our incomplete understanding of the functional processes that drive it. The latter uncertainty is further underlined by the potential over-fitting of some relationships with the retained covariates and the large confidence intervals surrounding them. Our use of proxy variables in place of direct drivers of distribution, coupled with the fact that we are not taking into account other important variables (such as prey availability, predator avoidance, and trophic competition) increases this uncertainty and may lead the models to potentially over-fit to their available observations. It should be noted, though, that dividing our observations across the three 'Habitat' categories means that there is a smaller number of observations per category, so for some of the extreme portions of the

covariate ranges, the estimated relationship is driven by fewer sightings and thus the certainty decreases.

Another possible reason our models retain multiple predictor variables and still show a relatively high degree of uncertainty around specific relationships could be the existence of sub-populations in offshore waters that is difficult to model. It is known that the “pelagic” bottlenose dolphin population in the Northeast Atlantic is genetically distinct from coastal populations (Mirimin et al., 2011; Louis et al., 2014a, 2014b), but there are not yet sufficient data to elucidate fine-scale population structure within the offshore population. If there are strong genetic differences, they could be driven by colonisation effects (Nykänen et al., 2018) or by habitat-specific foraging specialisations or mating/social structure. Aerial survey design generally makes it difficult to define groups of dolphins that may be well spread out, as is often done in boat-based surveys (e.g., usually animals within 100 m of each other are classed as one; Irvine et al., 1981; Rogan et al., 2019), let alone identify individuals to quantify social associations. For example, the bottlenose dolphins resident within the Shannon Estuary have been indicated to exhibit a more fluid social structure (Ingram 2000; Baker et al., 2018) than the ones ranging along the west coast of Ireland (‘casual acquaintances’ versus ‘long-term companions and casual acquaintances’, respectively; Nykänen, 2016; Nykänen et al., 2018) and this fine-scale population structure can either be a result of, or result in, different habitat use patterns. Detailed investigations of the pelagic population’s structure could shed some light on whether the patterns observed in the different ‘Habitat’ categories are a result of the entire population exhibiting variable behaviour according to where they are, or that subsets of the population range in different habitat types and therefore show different responses to the environmental predictors included in our models. The former case may be supported by the lack of any distinct distributional hiatus over the entire study area, although that could also be a result of ‘grey areas’ where adjacent sub-populations overlap.

In order to designate appropriate management units to meet the EU Habitats Directive requirements, it is critical to identify specific geographic regions with which bottlenose dolphins associate. While our results do not necessarily define specific geographic “hotspots” of habitat use that could be delineated as SACs, they do highlight how dolphin habitat use changes, both seasonally and depending on the specific habitat they are in. Our models did predict higher occurrence of dolphins along the southwest coast and the Porcupine Basin in the summer; these could be areas to target in future surveys and

consider in conservation and spatial planning schemes. There is scope for development of more accurate models, with the inclusion of more detailed biotic information if that becomes available. While including more predictors does not necessarily always improve model performance (Grecian et al., 2012; Critchley et al., 2018;), the inconsistent performance of the models in our study would argue that we have not sufficiently captured all the nuances of bottlenose dolphin habitat use in this region. Although the differences in numbers sighted were considerable between seasons and between years, the higher abundance estimates in the second survey season (Rogan et al. 2018) could be attributed to the influx of dolphins from beyond the extent of the study area—finding out how far and how quickly these animals range would be one way to assess whether or not that was the case. Furthermore, it would be important to distinguish whether the pelagic population of dolphins is, in fact, one population or multiple distinct ones, by doing finer-scale studies including photo-identification (for social structure analysis) and biopsy sampling (for genetic analysis) techniques. Identifying the environmental characteristics that these animals are more likely to be associated with could facilitate the targeted design of such fine-scale surveys, reducing the associated logistical and financial costs. Our study is, therefore, an important step towards the implementation of better monitoring methods for pelagic bottlenose dolphins in Irish waters (Figure 1.1a).

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APPENDIX IA

Table IA.1. Abundance estimates and associated coefficient of variation (CV) and 95% confidence intervals for the bottlenose dolphins sighted during each survey season (from Rogan et al., 2018a).

Season	Abundance estimate	CV	95% confidence intervals
Summer 1	12,633	33.81	6,609–24,148
Winter 1	35,399	22.06	23,021–54,434
Summer 2	87,330	20.70	58,029–131,426
Winter 2	212,646	15.49	157,026–287,967

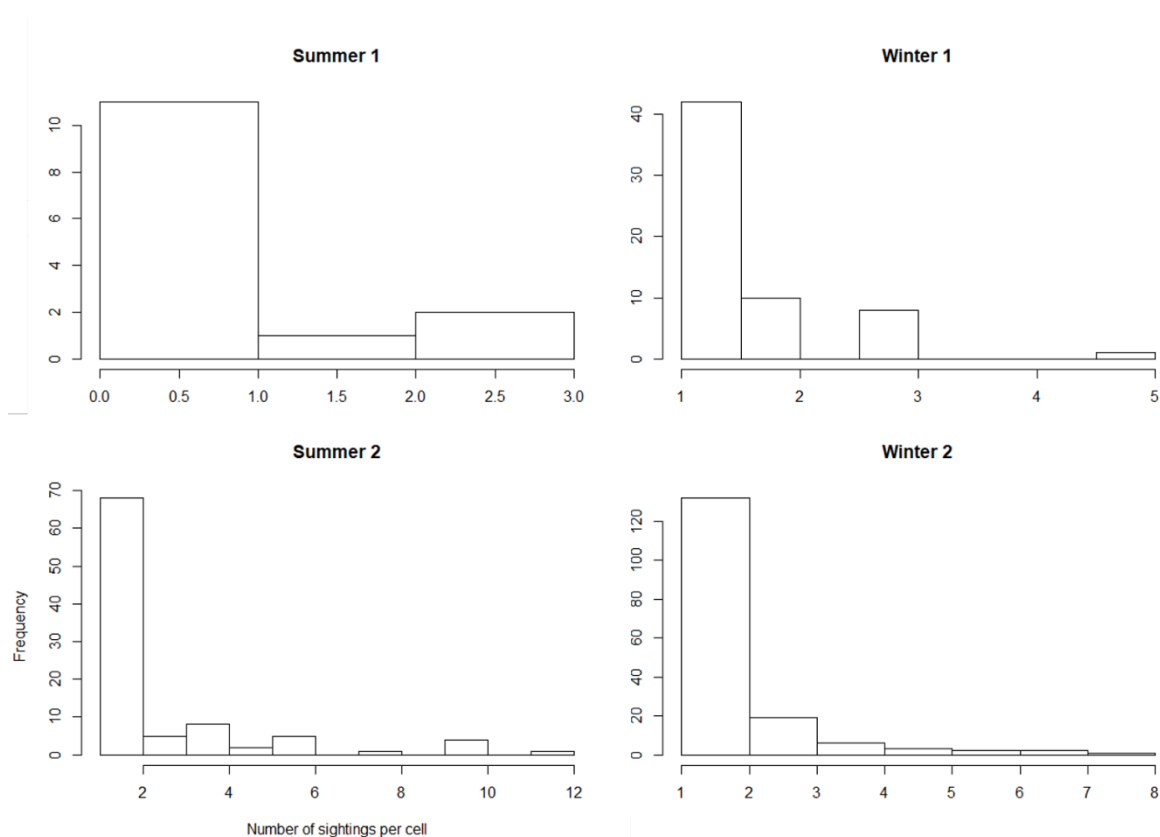


Figure IA.1. Frequency distributions of the number of bottlenose dolphin sightings in each grid cell of the modelled study area. Cells with no sightings were excluded from this graph, as the “0” bars would extend beyond the page length at this scale.

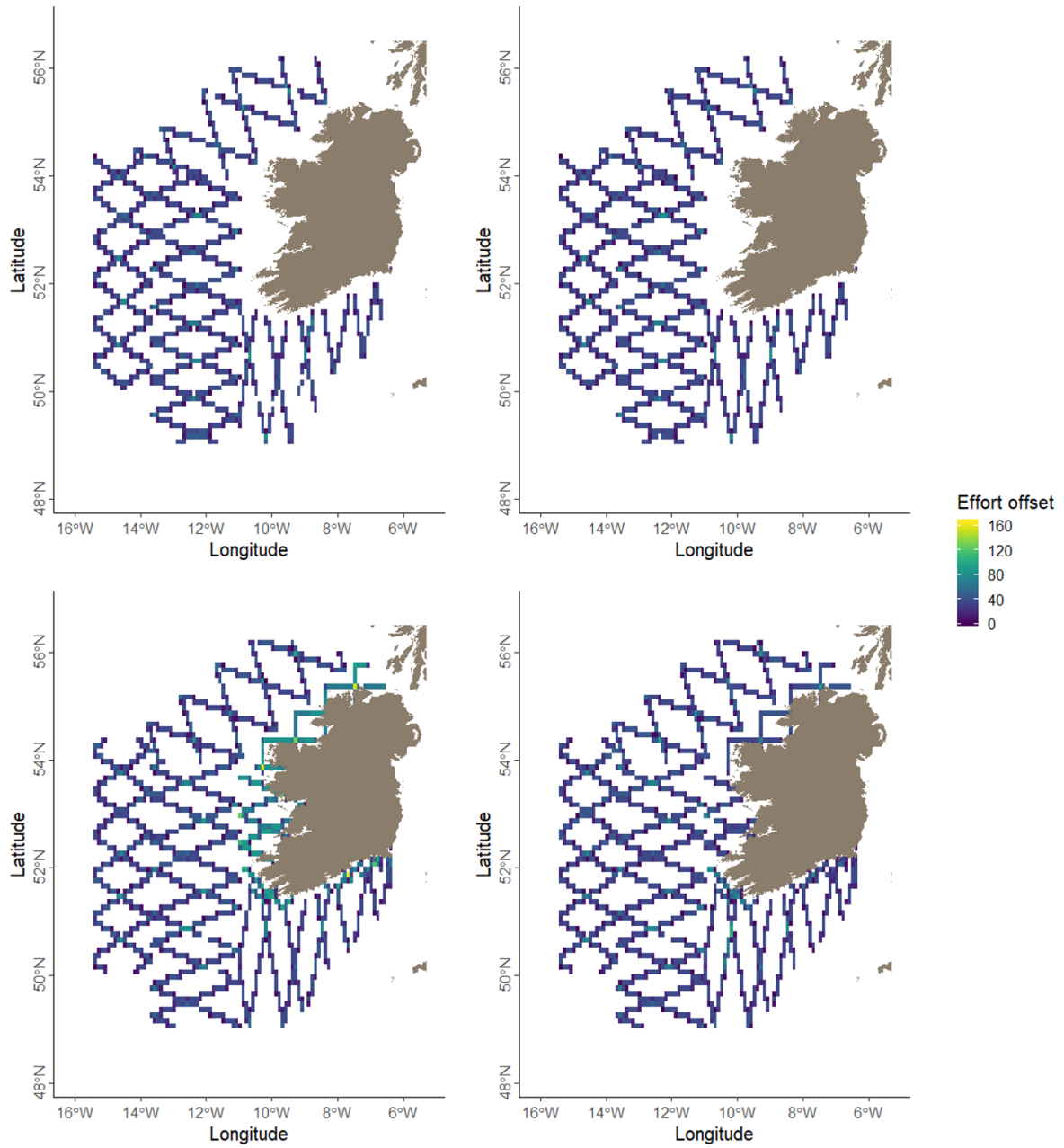


Figure IA.2. Effort offset per grid cell used in the GAMs to account for biases in dolphin detectability. The offset is equal to the length of the trackline traversing each cell, multiplied by twice the effective strip width calculated for bottlenose dolphins during these aerial surveys, which was dependent on Beaufort sea state.

APPENDIX IB

The following maps show predicted bottlenose dolphin occurrence in the Irish EEZ based on different GAMs that were trained on the second year of data (Summer 2 and Winter 2). Points indicate real observations in each season. Left column: lower 95% confidence intervals of prediction. Middle column: predicted probability of occurrence and real observations. Right column: upper 95% confidence intervals of prediction.

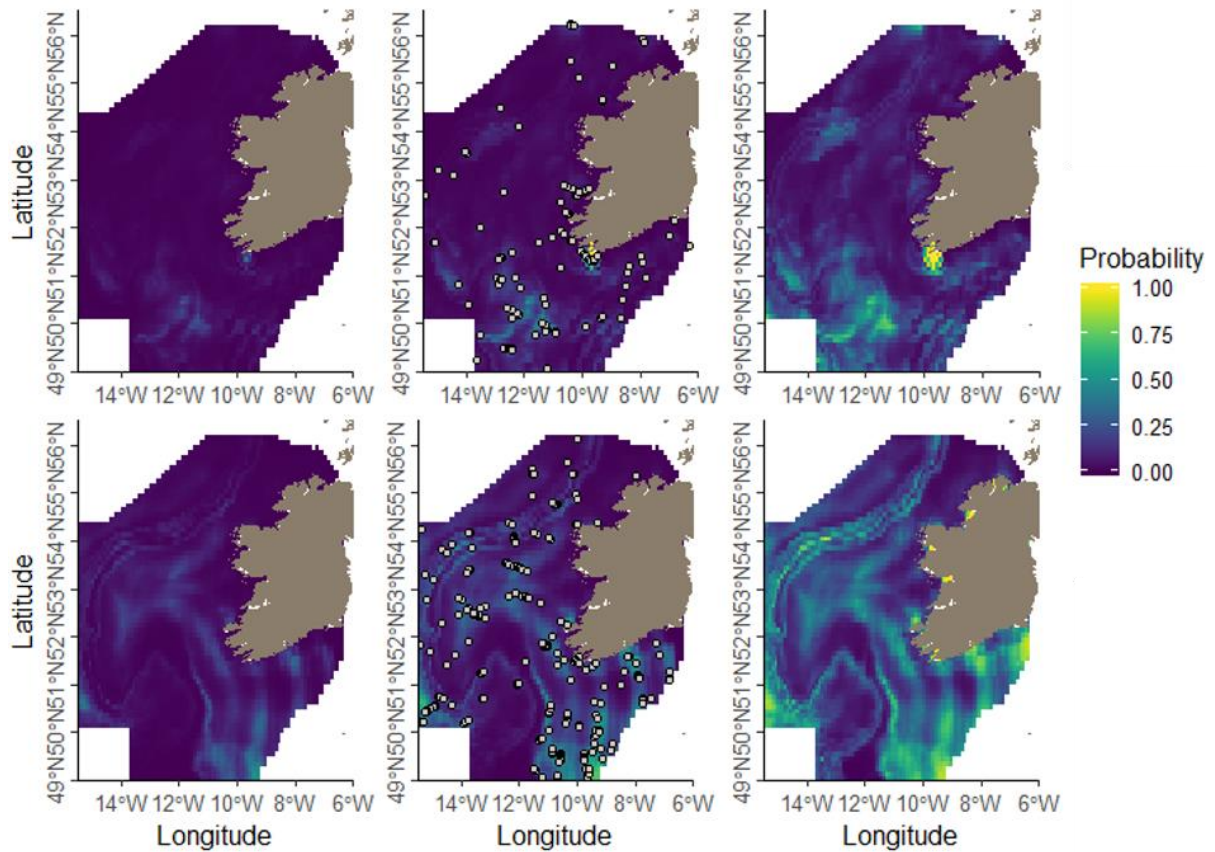


Figure IB.1. Predictions based on binomial GAMs not including a habitat classifier for Summer 2 (top) and Winter 2 (bottom).

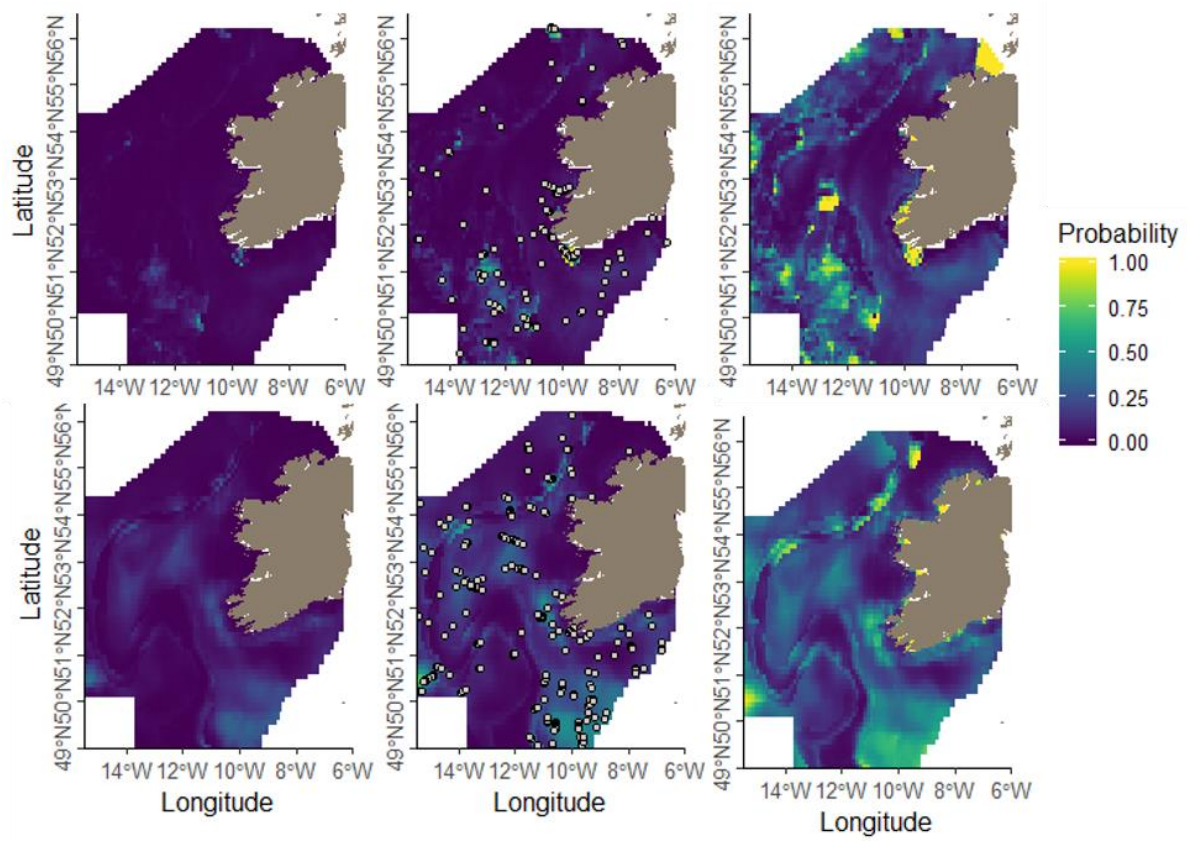


Figure IB.2. Predictions based on binomial GAMs including a habitat (Shelf, Slope, Abyss) classifier for Summer 2 (top) and Winter 2 (bottom).

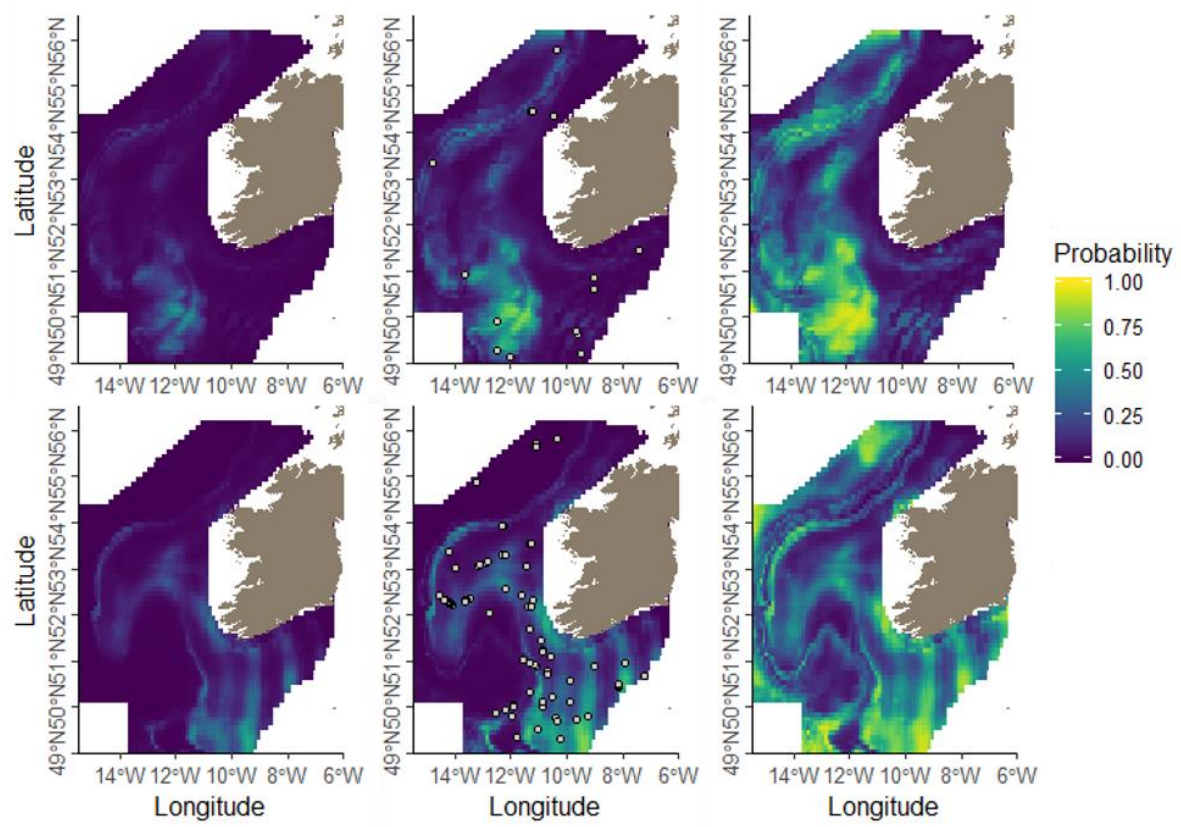


Figure IB.3. Retrodictions based on binomial GAMs not including a habitat classifier for Summer 1 (top) and Winter 1 (bottom).

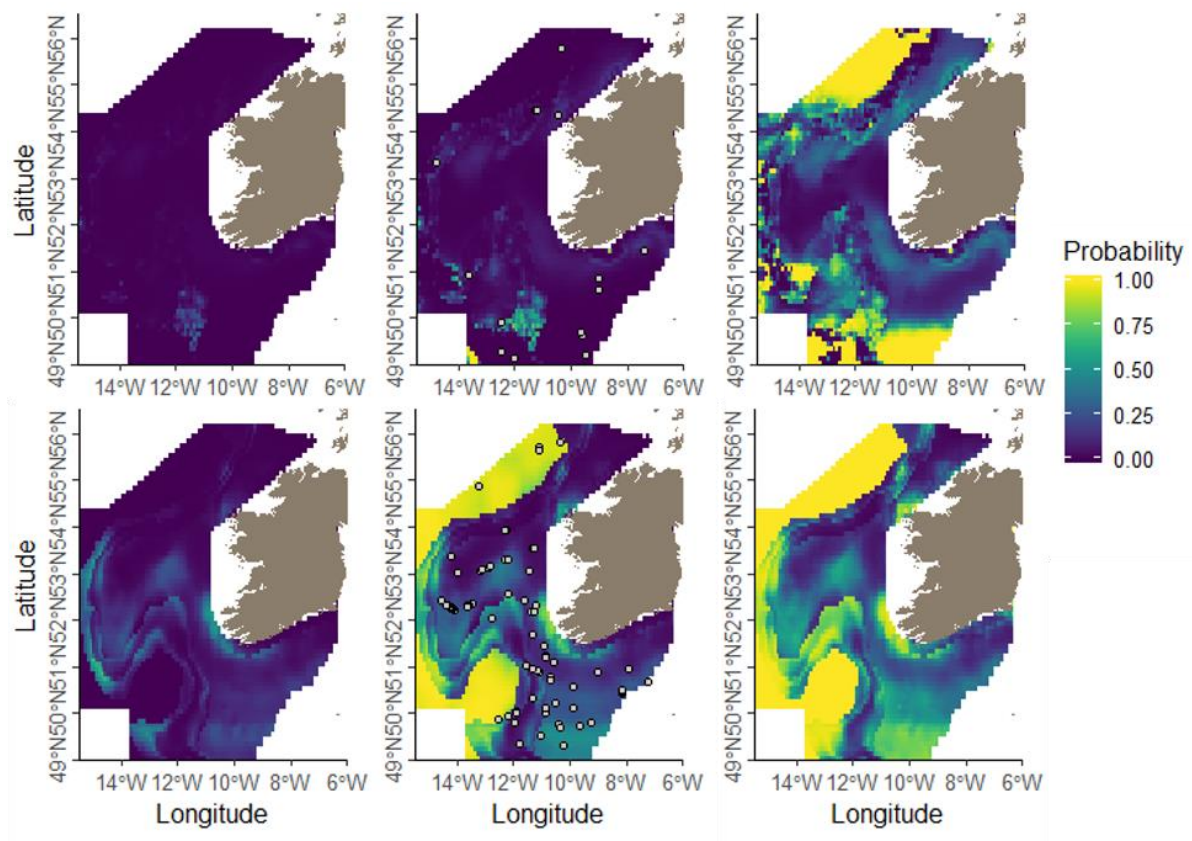


Figure IB.4. Retrodictions based on binomial GAMs including a habitat (Shelf, Slope, Abyss) classifier for Summer 2 (top) and Winter 2 (bottom).

Chapter 3. Site occupancy of a coastally ranging bottlenose dolphin population monitored through passive acoustic monitoring

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Photo: Breffni Gray

Author contributions:

1. Original placement of C-PODs, advice on R packages and GEE modelling.

ABSTRACT

Monitoring cetacean populations to ensure their favourable conservation status can be challenging, especially if they range in remote or difficult to access areas. A case in point is the population of bottlenose dolphins that ranges along the west coast of Ireland. While a Special Area of Conservation has been designated to protect two areas that are considered important for breeding and calving, the population's precise geographic range and habitat use patterns remain unknown. Passive acoustic monitoring, which allows continuous coverage with minimal upkeep, was used to monitor the site occupancy of these animals in two locations on the west coast, one within the SAC and one outside it. C-PODs were deployed from 2013 to 2017 and generalised additive models were used to investigate dolphin occurrence in relation to a suite of environmental parameters. Generalised estimating equations were used to account for temporal autocorrelation and models were run on three temporal scales, hourly, daily, and monthly, each incorporating different environmental covariates. The hourly model indicated higher dolphin occurrence with increasing tidal levels, while the daily model showed that dolphin presence peaked between September and October in one site and later in the year in the other. The monthly model showed that chlorophyll *a* concentration had a positive effect on dolphin detection rates in both sites, while sea surface temperature had a positive effect on dolphin occurrence only in the northernmost site. Although poor model fit in several cases highlights the gaps in our knowledge regarding environmental parameters that may be more influential, such as prey abundance, bottlenose dolphin habitat preferences are shown to be site-specific. This has implications regarding the long-term monitoring of this population and added protection measures outside the existing SAC.

3.1. INTRODUCTION

For long-term monitoring of species or populations, understanding their habitat use patterns in an area of interest is of paramount importance (MacKenzie et al., 2003). This can be particularly challenging for wide-ranging animals such as marine mammals, as their direct observation is not always possible or practicable, and the geographic ranges of a population are difficult to define. Therefore, describing site occupancy patterns in a given area provides vital information with respect to the importance of that area for that population (Durban et al., 2000). For populations that are particularly vulnerable to human disturbance, such as small populations of coastal cetaceans (McIntyre, 1999; Allen et al., 2012; Pirotta et al., 2015; Heiler et al., 2016; Marley et al., 2017), knowledge of distribution and occupancy is crucial for the mitigation of anthropogenic pressures.

Animal movements can be driven both by environmental and biological processes, and marine mammals in particular are known to be influenced by factors such as benthic topography (depth, slope, aspect, substrate type) (Cañadas, Sagarminaga, & García-Tiscar, 2002; Eierman & Connor, 2014; Pirotta et al., 2011), temperature, primary productivity, proximity to ocean fronts (Gomez & Cassini, 2015; Mannocci et al., 2014; Scales et al., 2014), prey availability, competition, foraging strategies (Doniol-Valcroze et al., 2012; Herr et al., 2016; Kopps et al., 2014), tidal parameters (Johnston, Thorne, & Read, 2005; Lin, Akamatsu, & Chou, 2013), and anthropogenic activities (Balmer et al., 2013; Bonizzoni et al., 2013). Some of these are static variables while others are subject to temporal fluctuations, and they can each affect cetacean distribution on different spatial and temporal scales (Ballance, Pitman, & Fiedler, 2006; Pirotta et al., 2014). Linking such external variables to cetacean habitat use helps us understand the drivers behind their movement and occupancy patterns and enables us to better design protection and management plans.

Passive acoustic monitoring (PAM) is a non-invasive method of gathering information on vocalising or echolocating species that can be difficult to detect visually, and has been successfully used to monitor various taxa, including birds (e.g., Oppel et al., 2014), insects (e.g., Penone et al., 2013), elephants (e.g., Wrege et al., 2012), primates (e.g., Kalan et al., 2015), and cetaceans (e.g., Van Parijs et al., 2009). The automated recording of vocalisations using devices that can be left in the field for prolonged periods of time reduces both the potential for human disturbance of the study species and the associated survey costs. Among the variety of PAM devices that have been developed for cetacean

surveillance over the years, the C-POD (Chelonia Ltd, Cornwall, UK) is a stationary, self-contained apparatus that can detect echolocation clicks produced by odontocetes, and is commonly used to monitor toothed whale populations, especially in coastal habitats. C-PODs consist of a hydrophone housed in a hard shell case, containing hardware and batteries. They are tethered to the seafloor, floating above the sediment, and detect sonar click trains (consecutive similar clicks at regular intervals) within a 300–400 m radius (conservative estimate, Nuuttila et al., 2013; Roberts & Read (2015) documented a maximum detection range of 933 m), logging the time, duration, inter-click intervals, dominant frequency, and other features that can be used to identify the sound source, onto an internal SD card. C-PODs have the advantage that they can be deployed for several months at a time—as they do not record actual sound, but rather particular sound features, the memory card does not fill up quickly, and the battery pack lasts for extended periods. The only logistical requirement is to retrieve the unit every few months in order to replace the batteries and download the data from the SD card, at which point the device can be re-deployed. The data are then processed with dedicated software and filtered to isolate the click trains produced by the species being studied. This is a cost-effective way to monitor specific sites for extended periods, providing valuable longitudinal data and insight into site occupancy patterns of echolocating cetaceans.

The common bottlenose dolphin (*Tursiops truncatus*) is listed under both Annex II and Annex IV of the EU Habitats Directive, which requires EU member states to maintain or restore the status of the species to a “favourable condition”. As part of this obligation, two Special Areas of Conservation (SACs) have been designated on the west coast of Ireland to protect known critical habitats for bottlenose dolphins, one in the Shannon Estuary (Lower River Shannon SAC) and one in Connemara (West Connacht Coast SAC) (Figure 3.1). The latter area is important for a coastally ranging population of bottlenose dolphins (Ingram, Englund, & Rogan, 2003; Nykänen et al., 2015) that is genetically and demographically distinct from other Irish populations (Mirimin et al., 2011; Nykänen et al., 2018). The abundance of this population was estimated at 189 individuals (CV=0.11; Nykänen et al., 2015), and the population is thought to be highly mobile along a considerable portion of the west coast, extending beyond the SAC boundaries at least as far north as Co. Donegal. Their wide geographic ranging patterns, coupled with the logistics of accessing multiple remote regions of the coastline, make acoustic monitoring an attractive, cost-effective option for collecting long-term information on site occupancy. Such information can then potentially be used to plan the timing of visual surveys for abundance monitoring.

Nykänen (2016) investigated temporal trends in dolphin occupancy using C-PODs at two key locations on the west coast of Ireland. Monitoring of these sites was continued for the present study, with the aim of examining the effect of environmental parameters on temporal patterns in click train detections and dolphin site occupancy.

3.2. MATERIALS AND METHODS

3.2.1. Study sites

C-PODs (Chelonia Ltd.) were deployed in two locations on the west coast of Ireland (Figure 3.1), based on results from studies on bottlenose dolphin habitat use (Ingram, Englund, & Rogan, 2001; Oudejans et al., 2010) and continuing acoustic data collection started by Nykänen (2016). The first was placed at the mouth of Killary Fjord, Co. Galway. This is one of three glacial fjords in Ireland, and is located within the West Connacht Coast SAC; it is approximately 15 km long and 0.75 km wide, with an average depth of 15 m. Several shellfish farms lie within the fjord itself, and a salmon farm is located directly outside its mouth (approximately 1500 m from the C-POD deployment site). Small scale fisheries operate outside the fjord, while its tributaries are important recreational salmon (*Salmo salar*) fishing spots. The second C-POD was deployed in McSwyne's Bay, Co. Donegal. This bay is approximately 8 km wide, with an average depth of 20–35 m. Salmon and mussel (*Mytilus edulis*) farms are also located in this area, and Ireland's leading fishing port, currently developing into an important cargo facility, is situated across the bay from the C-POD's anchorage.

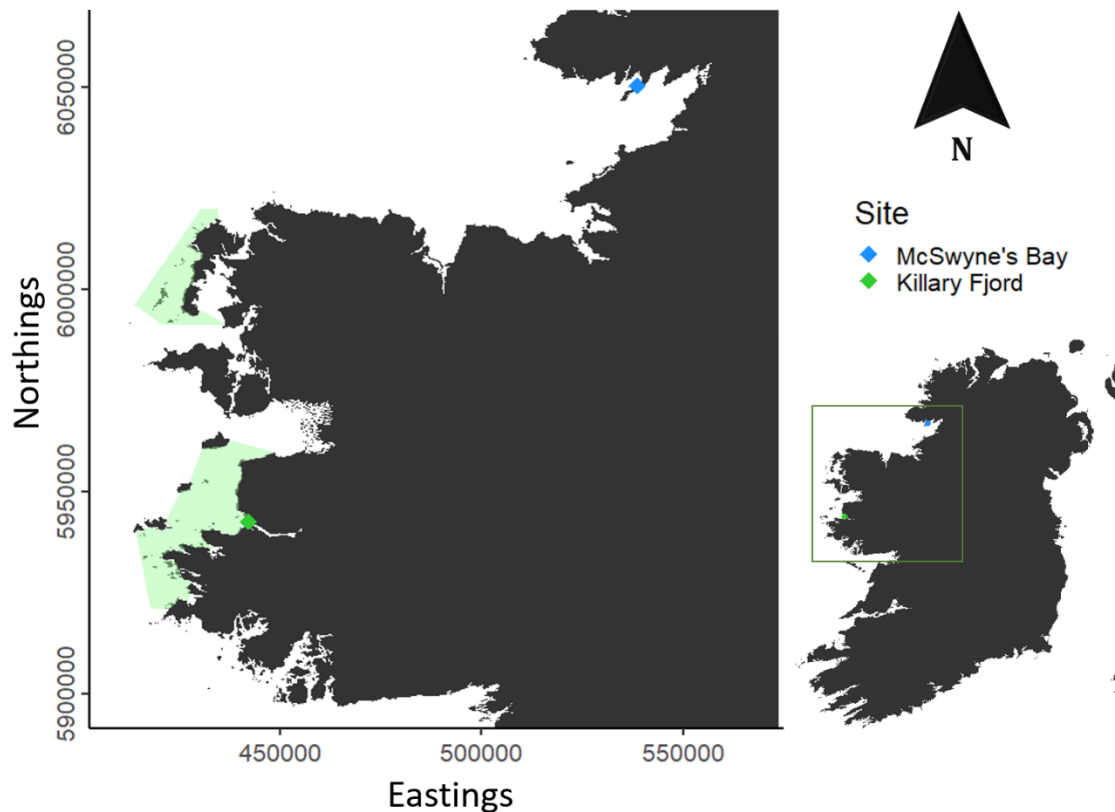


Figure 3.1. Deployment sites of the two C-PODs on the west coast of Ireland (inset) in relation to the West Connacht Coast SAC (light green polygons).

3.2.2. C-POD deployment

As the click train filter of the acoustic detection software used cannot distinguish between different delphinid species, both C-PODs were anchored very close to shore to minimise the possibility of detecting delphinids other than bottlenose dolphins (Perrin, Würsig, & Thewissen, 2002; Bearzi et al., 2003). Each was tethered to the seafloor by a chain and rope system attached to a large cement block, allowing them to float upright 2–3 m above the seabed, in water depths of 6–12 m at low tide. The C-POD in McSwyne's Bay was originally deployed on October 19, 2013, while the one in Killary was deployed on September 15, 2014. Each site was visited every 4–6 months (subject to weather and tide conditions), whereupon the C-PODs were retrieved, the data downloaded and batteries replaced, and they were re-deployed as soon as possible after maintenance (ropes and attachments checked/replaced, biofouling removed, O-rings cleaned). I took over responsibility for the data collection in April 2016.

3.2.3. C-POD data processing

Data downloaded from the memory cards were processed in C-POD.exe software (Chelonia Ltd.) to filter echolocation clicks from boat engine and environmental noise (e.g. sediment movement). To discriminate between high frequency harbour porpoise (*Phocoena phocoena*) clicks and broadband dolphin clicks and to maximise detection of dolphin click trains, the Generalised Encounter Classifier (GENENC) classifier and “Other cet” click trains of high and moderate quality were selected (N. Tregenza, Chelonia Ltd, pers. comm.). These filters, in addition to placement of the C-PODs close to shore, reduce the occurrence of false positives (Roberts & Read, 2015), maximising the likelihood that the detections used in the final analysis were of bottlenose dolphins, rather than of common (*Delphinus delphis*), striped (*Stenella coeruleoalba*), or Risso’s (*Grampus griseus*) dolphins.

3.2.4. Environmental variables

The presence/absence of dolphin echolocation click trains or detection positive minutes (DPMs) were tested against a suite of environmental covariates, which were selected based on their potential or known effects on the distribution of marine top predators (Lin et al., 2013; Manna, Manghi, & Sarà, 2014; Pirotta et al., 2015; Cox et al., 2016). To determine the existence of tidal or diurnal patterns in dolphin presence, predicted hourly tide level data (in m) and sunrise and sunset times for each study site were obtained via POLTIPS software (NERC National Oceanography Centre, Liverpool, UK). A two-level “daylight” factor was calculated from the sunrise and sunset times for each day, binning the observation times into either “Light” (between sunrise and sunset) or “Dark” (between sunset and sunrise). To assess the influence of freshwater runoff, monthly rainfall data (in mm) were downloaded from Met Éireann’s archive (met.ie/climate/available-data/historical-data). Monthly remotely sensed chlorophyll *a* (chl, in mg m⁻³) and sea surface temperature (SST, in °C) were downloaded from NASA’s website via the GIOVANNI portal (<http://giovanni.gsfc.nasa.gov/giovanni/>), from their MODIS Aqua sensor. As the study sites were close to shore, satellite data were not always available for their precise location, so the values were taken from a larger 8 x 8 km area around each deployment spot.

3.2.5. Modelling dolphin site occupancy over time

The R version 3.5.2 (R Core Team, 2018) packages *mgcv* (Wood, 2017) and *MRSea* (Scott-Hayward et al., 2013) were used to fit generalised additive models (GAMs) to the echolocation and environmental data. Due to the different temporal resolution of the various environmental covariates, three separate GAMs were run, dividing the explanatory variables into an hourly, a daily, and a monthly model.

The hourly model included factors “Daylight” and “Site” and continuous variables “Hour of the Day” and “Tidal level”. In the hourly model, the response variable was modelled as presence/absence of echolocation click trains. Due to the poor fit of count data (DPM/h) to Poisson, quasi-Poisson, or negative binomial distributions and the overdispersion of the residuals, a quasi-binomial distribution with a “logit” link function was applied.

The daily model included factors “Site” and “Year” and a continuous “Day of the year” variable. The response variable here was modelled as DPM per day with a quasi-Poisson distribution and a “log” link function, as it showed the least overdispersion compared to other distributions.

The monthly model included continuous covariates “chl”, “SST”, and “Rainfall”, and factors “Site” and “Year”. The response variable was modelled as detection positive days (DPDs) per month, also with a quasi-Poisson distribution and “log” link function.

The covariates included in each model were tested for collinearity using variance inflation factors (VIF). An autocorrelation function (ACF) plot was used to visually check the level of temporal autocorrelation in the data. To account for this serial autocorrelation, mixed effects GAMs (GAMMs) with an appropriate correlation structure were fit to the data. In some cases this proved computationally impracticable, and so generalised estimating equations (GEEs; Liang & Zeger, 1986) were applied using the “MRSea” package after fitting GAMs with the same package. GEEs with various autocorrelation structures were tested, and the most appropriate one was selected based on the lowest QIC value.

3.3. RESULTS

In combination, the two C-PODs actively recorded for a total of 41,030 hours and logged 9288 DPMs (with a minimum of one dolphin echolocation click train detected during a minute of surveillance) (Table 3.1). The number of detection positive days per month is shown in Figure 3.2. In general, the number of detection positive days was higher in Killary

Fjord than in McSwyne's Bay, with the exception of the month of May 2016. Dolphins were recorded in every month when the loggers were active, except for January and February 2015 in Killary Fjord.

Table 3.1. C-POD deployment summary for each of the two study sites, showing the number of deployment days, number of detection positive days, and number of detection positive minutes per year.

Year	Deployment days		Detection positive days		Detection positive minutes	
	McSwyne's Bay	Killary Fjord	McSwyne's Bay	Killary Fjord	McSwyne's Bay	Killary Fjord
2013	74	0	14	0	237	0
2014	314	108	81	32	2218	261
2015	260	265	46	152	665	3219
2016	156	226	30	97	487	1018
2017	0	310	0	115	0	1183
Total	804	909	171	396	3607	5681

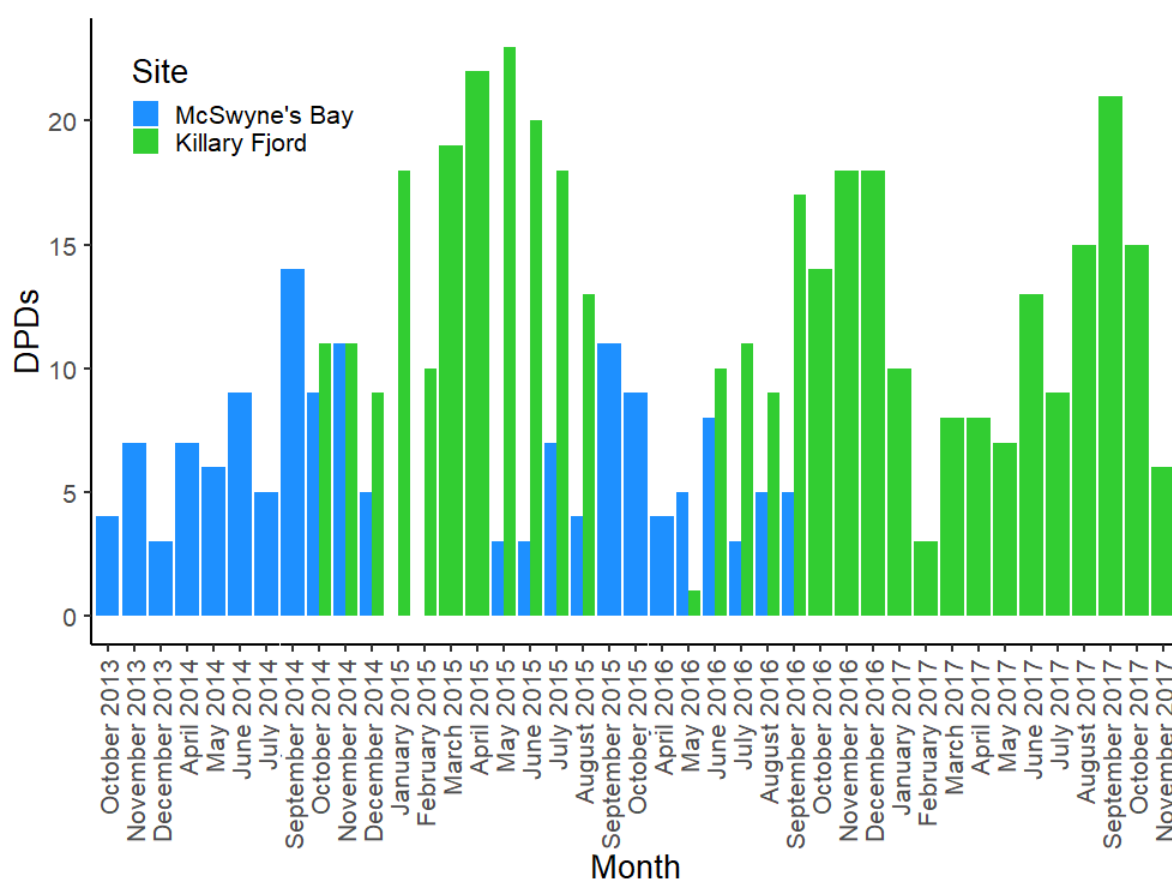


Figure 3.2. Detection positive days (DPDs) per month recorded by C-PODs in each of the two study sites during deployment (2013–2017). Thick bars denote months in which the C-POD in the other location was not recording click trains. Thin bars denote months in which both C-PODs were recording. In January and February 2015, there were no dolphin detections in McSwyne's Bay.

3.3.1. Hourly model

There was significant positive temporal autocorrelation in the hourly model's residuals (Run's test statistic: -185.41, $P < 0.0001$). After inspecting the autocorrelation plots of the initial model residuals, the data were divided into consecutive weekly blocks, between which the autocorrelation was reduced to zero (Figure 3.3). The within-block weekly autocorrelation was modelled with GEEs; the “first-order autoregressive” correlation structure was selected over the “exchangeable” and “working independence” structures based on lowest QIC value (12050.9, 12066.5, 12051.4, respectively).

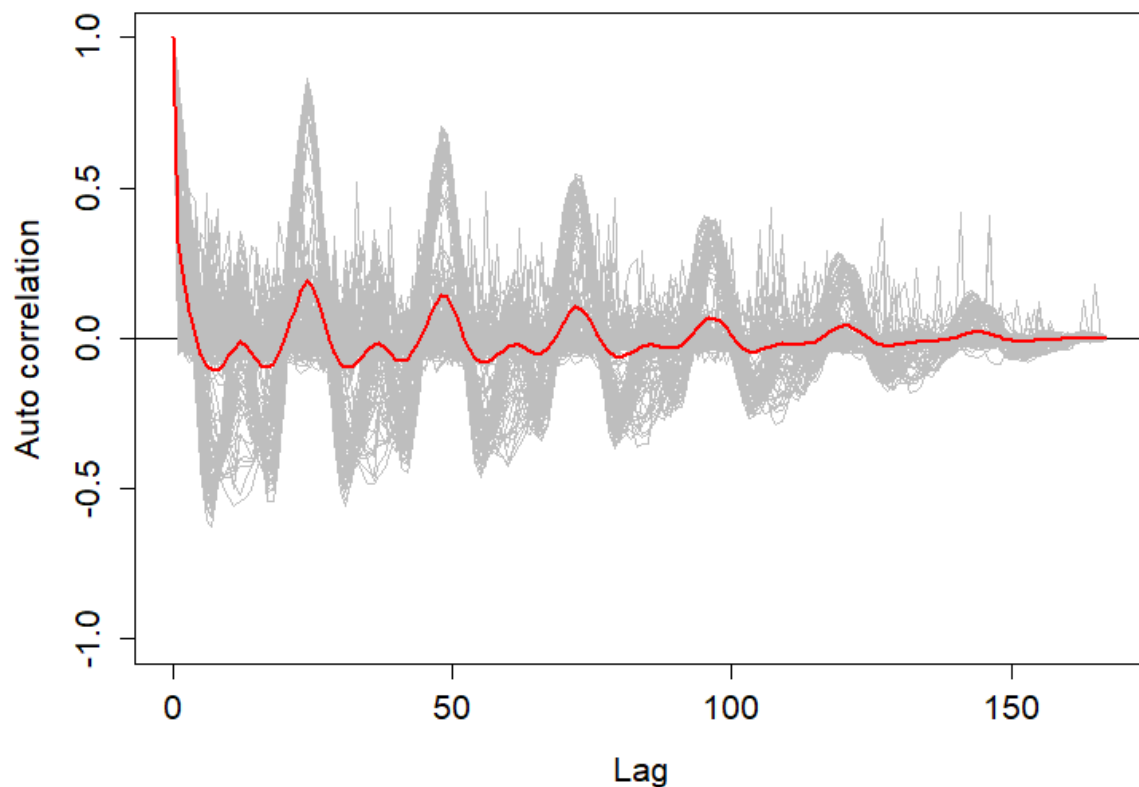


Figure 3.3. Correlation of the hourly GAM residuals for each block (grey lines) and mean autocorrelation at each lag (red line). Lag is given in hours (150 h = 6.25 days); autocorrelation values >0.5 denote significant positive autocorrelation and values <-0.5 significant negative autocorrelation.

Site and Tidal level were retained as significant explanatory variables in the best-performing model (Table 3.2), with a higher probability of dolphin detection in Killary Fjord than in McSwyne's Bay ($P < 0.0001$) and dolphin detection probability increasing at water levels >5 m above chart datum ($P < 0.0192$) (Figure 3.4). However, the low marginal R^2 (0.0066) and concordance correlation (0.013) values are indicative of very poor model fit and predictive power.

Table 3.2. Model setup, showing the variables included in each initial model. * denotes significant variables retained in each model.

Model	Response variable	Predictor variables	
		Factors	Continuous
Hourly	Presence of click trains/hour	Daylight, Site*	Hour of the day, Tidal level*
Daily	DPM/day	Site*, Year*	Day of year*
Monthly	DPD/month	Site*, Year	chl*, SST*, Rainfall

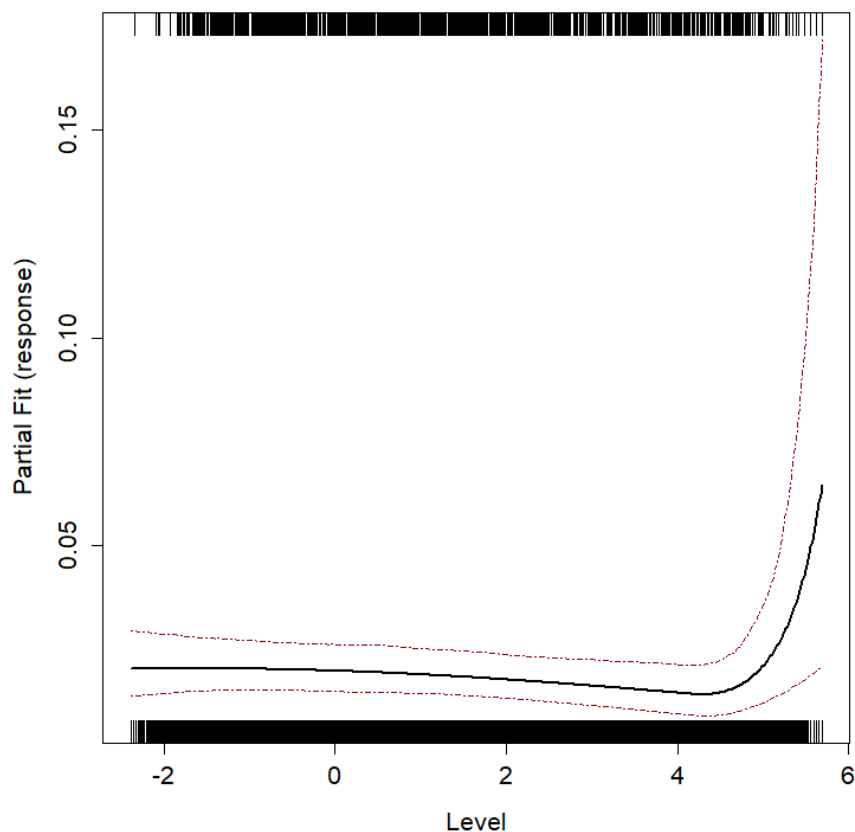


Figure 3.4. Partial residual plot of the binomial GAM-GEE model for dolphin detection probability and the remaining significant explanatory continuous covariate “Tidal level” (in m above chart datum). Solid line is the estimated fit, red dotted lines denote the 95% confidence intervals, rugs on the x axis show observed data values, with the presence on the upper part of the plot, and absence on the lower part.

3.3.2. Daily model

Inspection of the residuals in the daily model showed a significant 20-day lag in correlation (Run’s test statistic: -40, $P < 0.0001$). Using a 20-day blocking approach, the ACF plot shows that correlation is minimised between those blocks (Figure 3.5), hence the blocking structure was considered appropriate for use in the GEE. A “working independence”

correlation structure was chosen based on the lowest QIC value when tested against “first-order autoregressive” and “exchangeable” structures (-16195.8, -15113.2, -16088.1, respectively).

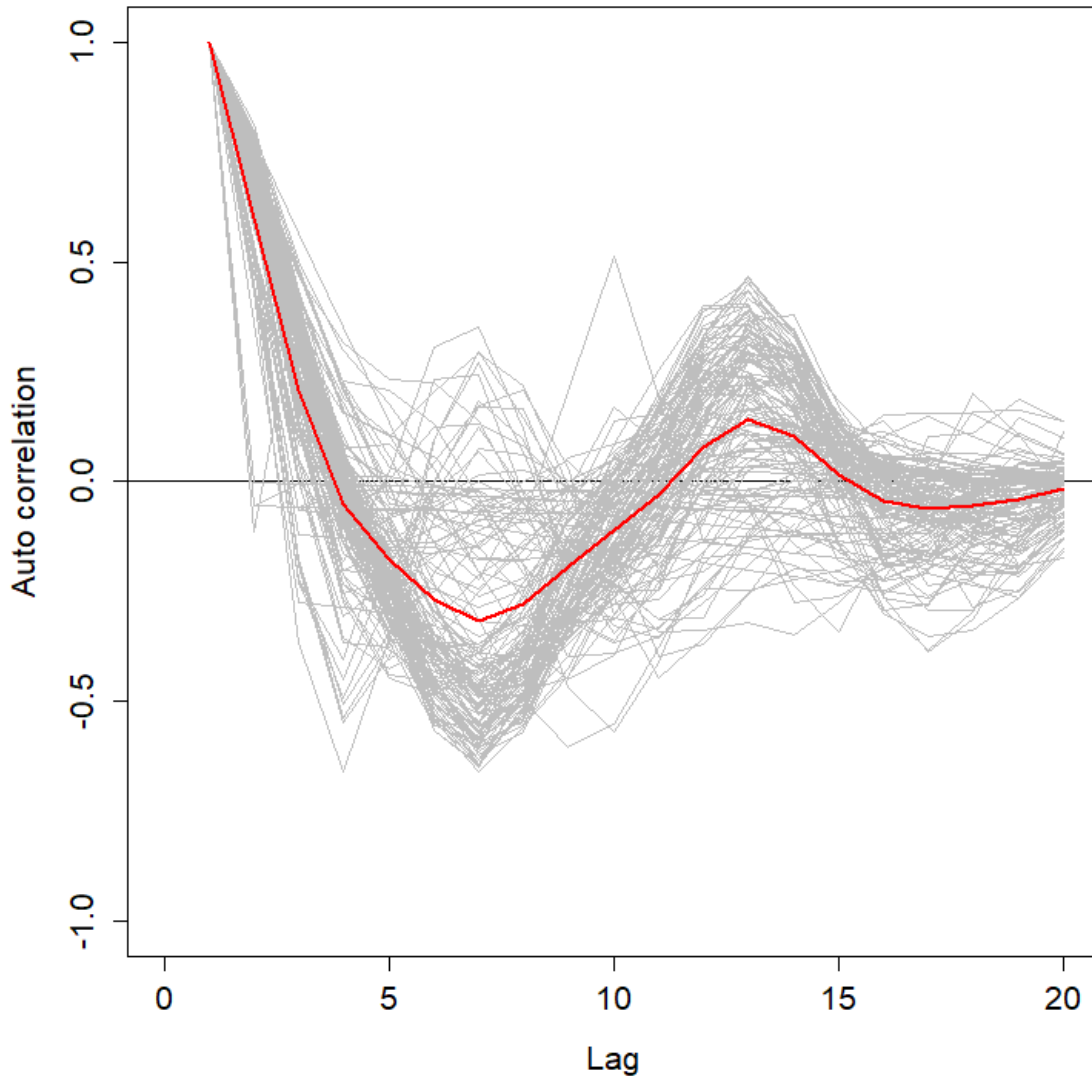


Figure 3.5. Correlation of the daily GAM residuals for each block (grey lines) and mean autocorrelation at each lag (red line). Lag is given in days; autocorrelation values >0.5 denote significant positive autocorrelation and values <-0.5 denote significant negative autocorrelation.

The daily model retained Day of year as a significant explanatory variable (Table 3.2), with dolphin detections peaking from September to October in McSwyne’s Bay ($P<0.001$) and increasing towards the end of the year in Killary Fjord ($P=0.007$), the latter trend being weaker than the former (Figure 3.6). Year and Site were also retained as significant covariates, with more DPMs per day in 2015 than in other years ($P=0.001$) and in Killary

Fjord than in McSwyne's Bay ($P=0.004$). However, the model's low concordance correlation value (0.0921) and marginal R^2 (0.0421) are again indicative of poor fit.

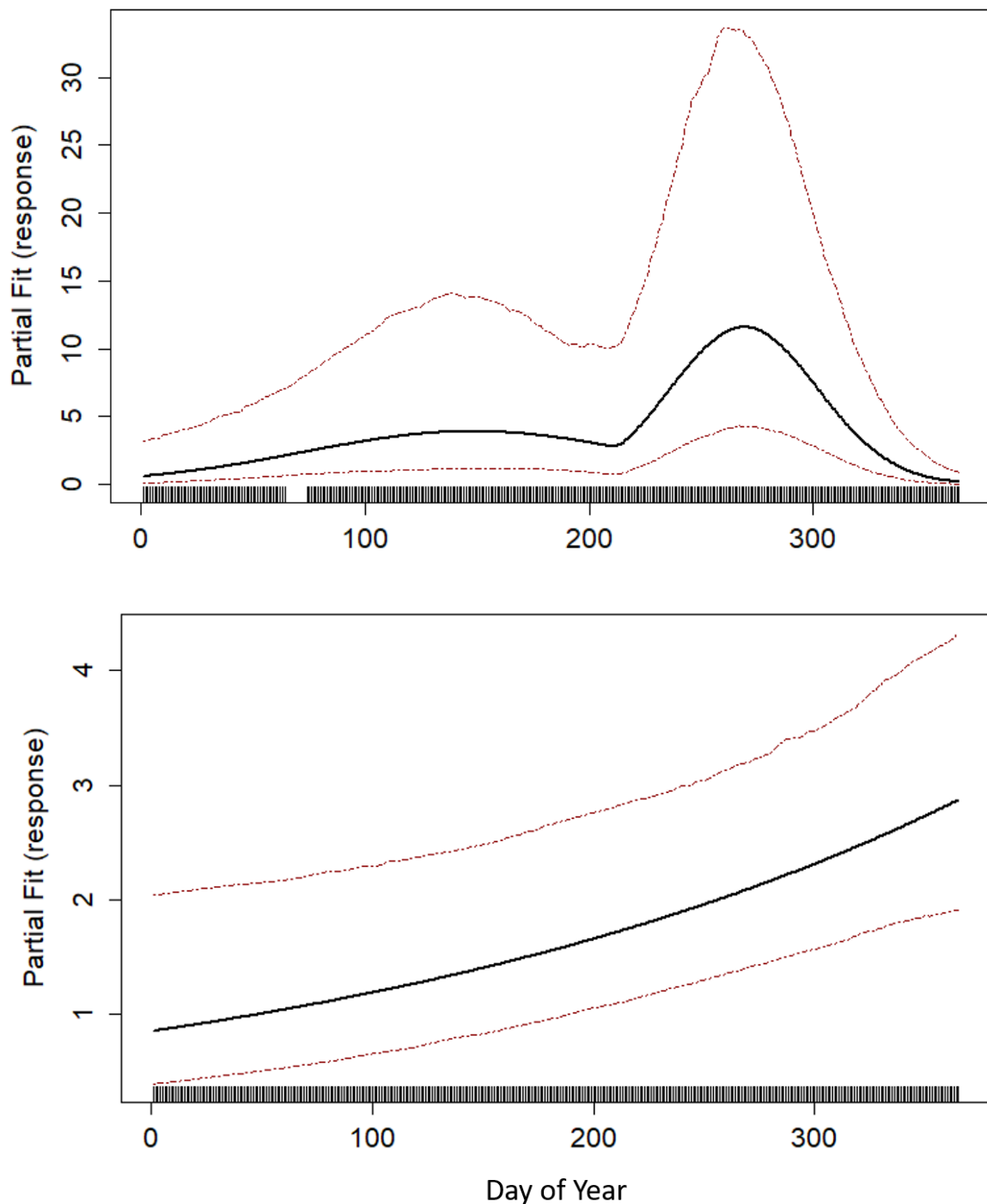


Figure 3.6. Partial residual plot of the GAM-GEE model for detection positive minutes per day and the remaining significant explanatory continuous covariate “Day of year” for each of the two C-POD deployment sites, McSwyne’s Bay (top) and Killary Fjord (bottom). Solid line is the estimated fit, red dotted lines denote the 95% confidence intervals, rugs on the x axis show observed data values.

3.3.3. Monthly model

The monthly model residuals showed some low autocorrelation (negative Run's test statistic: -1, $P=0.2$), but it was resolved by using a mixed GAM approach with a “first-order autoregressive” correlation structure (corAR1). Chlorophyll *a* showed a positive correlation with the number of days dolphins were present in both McSwyne's Bay ($P=0.051$) and Killary Fjord ($P=0.097$). SST was retained as a significant predictor of dolphin detections in McSwyne's Bay ($P=0.021$), showing a positive correlation with DPDs, but not in Killary Fjord ($P=0.582$) (Figure 3.7). Site was also a significant factor term, with more DPDs in Killary Fjord than in McSwyne's Bay. Rainfall was dropped from the model entirely, as it was not an informative variable in either location (Table 3.2). The model diagnostics (residual plots, $R^2=0.334$) are indicative of good model fit.

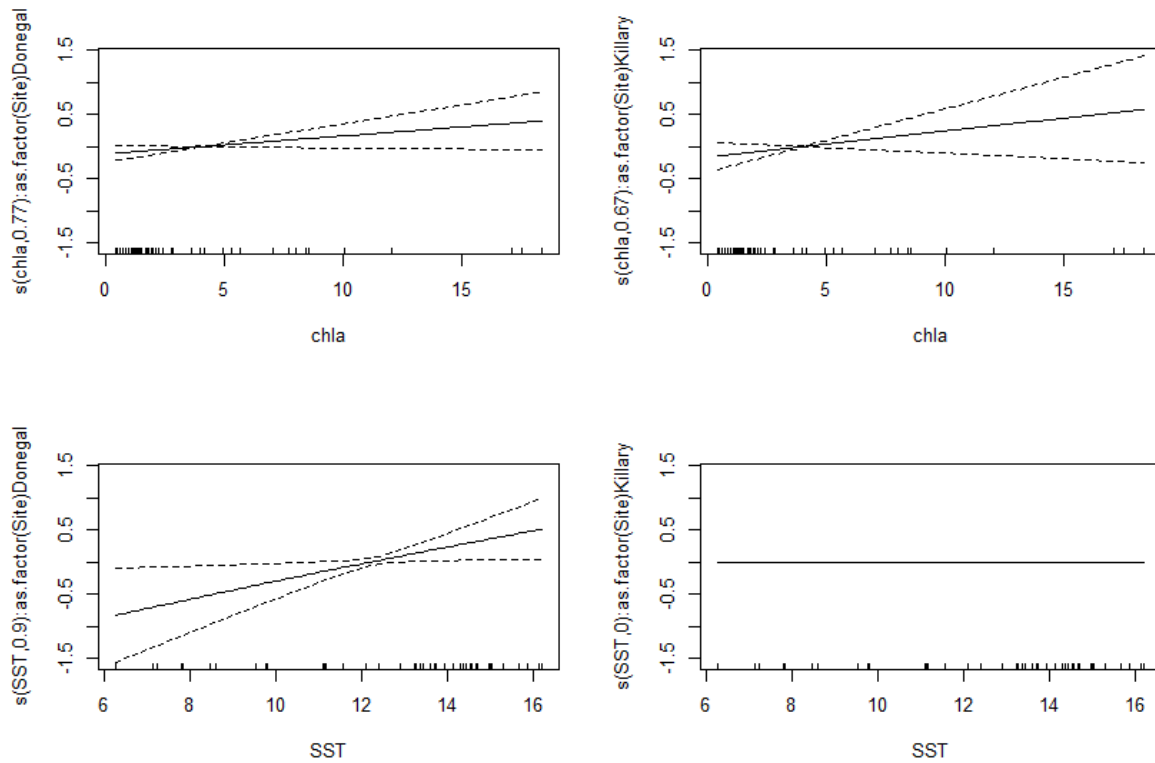


Figure 3.7. Estimated smoothing curves of the relationship between detection positive days and significant environmental variables for GAMMs of each of the two C-POD deployment sites, McSwyne's Bay (left) and Killary Fjord (right). Chla: chlorophyll *a* content; SST: Sea surface temperature. Solid lines are the smoothers, rugs on the x-axis denote observed covariate values, dotted lines indicate the 95% confidence intervals. Note that SST is not an informative predictor of variation in DPDs per month in Killary Fjord, hence the horizontal line and lack of confidence intervals. Y-axis shows strength of the effect of the predictor, with estimated degrees of freedom in brackets.

3.4. DISCUSSION

Understanding patterns in habitat use, occupancy rates, and their environmental drivers is a useful step towards defining and monitoring protected areas for marine top predators. A passive acoustic monitoring setup was deployed here to gather information on bottlenose dolphin site occupancy in two locations on the west coast of Ireland, one situated within SAC boundaries and one outside the protected area. Echolocation click trains detected by C-PODs were modelled in relation to a suite of environmental predictors at three temporal scales.

While diel patterns in detections have been observed in some dolphin species and harbour porpoises (Benjamins et al., 2016; Temple et al., 2016; Williamson et al., 2017), hour of the day was not retained as a significant predictor of dolphin detections in this study, despite a strong 24-hour pattern being apparent in the ACF plot (Figure 3.3). This accords with a study carried out on bottlenose dolphins in the Shannon Estuary (Philpott et al., 2007). Further, Wells et al., (2013) describe the foraging and travelling activities of bottlenose dolphins in Sarasota, Florida, as not changing significantly between day and night; however, their echolocation click rates did show some diurnal patterns, peaking during night-time and early morning/late evening hours. It thus appears that quotidian patterns in habitat use, or at least in echolocation, are highly site-specific.

Concordant with other studies (e.g. Philpott et al., 2007; Temple et al., 2016; Nuuttila et al., 2017), the probability of dolphin detections in this study was influenced by the tidal state. According to the hourly model, the detection probability increased with increasing water level of >5 m above chart datum. Similarly, high and flood tides were also significant predictors of the presence of *Tursiops aduncus* and *Sousa plumbea* in Zanzibar, Tanzania (Temple et al., 2016), whereas in the Shannon Estuary, Ireland, more dolphin echolocations were detected in the first four hours of the ebb tide (Philpott et al., 2007), and in Cardigan Bay, Wales, bottlenose dolphins were more often detected closer to low tide and shortly after sunrise (Nuuttila et al., 2017). Therefore, much like the diel variation in dolphin presence, there appears to be considerable site-specific variation in the response of dolphins to the tidal state. These differences may relate to foraging activity and the distribution and abundance of prey species. For example, the timing of migrating Atlantic salmon has been linked to high water and flood tides, with smolts remaining in place during flood tide phases (when the current is against their seaward movement) (Lacroix & McCurdy, 1996) and adults' positions oscillating with the tide, moving with the

prevailing tidal currents (Aprahamian, Jones, & Gough, 1998). Salmon likely constitute an important part of bottlenose dolphin diet in Irish waters, having been found in the stomachs of stranded animals (Hernandez-Milian et al., 2015) and observed being chased and tossed by dolphins both in the Shannon Estuary and Killary Fjord. Predictable prey movements, such as the upstream migration of salmon, could be readily exploited by a top predator known to adapt its foraging strategies to targeted prey (Ansmann et al., 2012; Pennino et al., 2013), and could therefore explain the higher detection probability observed in this study at higher water levels. However, it is also possible that sound travels further at higher tidal levels (T. Doyle, pers. comm.), so the detection range of the C-PODs increases at high/spring tides, resulting in increased click detections. It would be beneficial to conduct a range test with playback of recorded clicks at different distances for each tidal phase, to see if this is a confounding factor.

In the daily model, the dolphin detections increased towards the end of the year in Killary Fjord, while they peaked between mid-September and mid-October in McSwyne's Bay. The change in detection rate could be explained by a change in the presence of the animals, or it could be due to a change in behaviour, i.e., where the animals are present but not echolocating. Seasonal variation in bottlenose dolphin presence and behaviour has been found in other areas, such as the northwestern Levantine Sea, Turkey (Baş et al., 2016) and Bahía San Antonio, Argentina, where Vermeulen, Holsbeek, & Das, (2015) found that socialising and surface feeding were more common in winter than in summer. The authors hypothesised that these variations are linked to prey seasonality, which could also explain the differences in site use in the present study. If dolphins are attracted to the study sites or behave differently because of variation in prey abundance, this could be reflected by their echolocation patterns. Killary Fjord's tributary rivers are important salmon and trout habitats, so it is possible that dolphins are attracted to that location following the summer grilse migration. In McSwyne's Bay, similar prey movements may attract dolphins to the area in September, but, as the monthly model shows, they may move away from the area when SST drops, leading to fewer detections during the winter months. Since SST was not a significant variable in Killary Fjord, it is possible that the dolphins in each area feed on different prey types. The monthly model also showed a marginally significant increase in dolphin detections with primary productivity, a proxy for prey availability. Therefore, the movements of dolphins are likely to reflect prey availability in both of the study sites. However, future efforts should focus on obtaining direct estimates of prey availability and distribution and include these in the site occupancy models in order to verify this.

Garrod et al. (2018) reported a very low mean false positive detection rate of 0.003% when using C-PODs, indicating that echolocation can be considered as a reliable proxy for dolphin presence and guaranteeing that they are present when click trains are detected. However, this does not necessarily mean that they are absent when no echolocation clicks are recorded. Echolocation rates have been found to vary between behavioural states, group size and the habitat type dolphins were observed in, with single animals echolocating at higher rates than groups of dolphins, and foraging animals echolocating more than non-foraging animals (Jones & Sayigh, 2002; Nowacek, 2005). The two study areas have very different hydrographic and seabed properties, with Killary Fjord having a steeply sloping incline and muddier substrate than McSwyne's Bay. This could influence the distribution of different prey species, and thus not only the amount of foraging that takes place in each area, but also the foraging strategies used—both of these factors could influence echolocating frequency and, thus, the number of DPMs recorded. Nuuttila et al., (2013) found that single animals are far more likely to be acoustically detected than groups and that detection probability decreases with larger group sizes. Although the animals detected in both sites likely all belong to the same coastal population (Nykänen et al., 2018), larger groups have been observed in McSwyne's Bay than in Killary Fjord (Nykänen et al., 2015); this could explain the consistently lower number of detections in the former site than in the latter. There are a number of factors that could generate false negatives in our dataset, e.g., the GENENC classifier, the high directionality of click trains, and the fact that C-PODs do not log echolocation unless an event contains five or more successive clicks with similar inter-click intervals. However, Philpot et al. (2007) found that 80% of the dolphins they sighted within 500 m of a T-POD were also detected acoustically, regardless of their behavioural state. Thus, it would seem that the likelihood of false negatives is minimal and that echolocation can be considered a robust proxy of dolphin site occupancy.

The diagnostics for the daily and weekly models showed fairly poor fit. This could be due to overdispersion of the model residuals, with no distribution family entirely appropriate for these data. On the other hand, it could also be due to the inability of a single model to capture all the nuances of environmental variables and their effects on dolphin occupancy, especially since the ones used are not necessarily directly linked to dolphin prey abundance and distribution. It is also likely that some important drivers (e.g., prey abundance or predator avoidance) behind the variation in dolphin detection were not included in the models. Furthermore, the effect of tidal height and direction on the distance sound travels

underwater could pose a confounding factor in the relationship between tidal level and detection probability. However, the monthly model fitted the underlying data well, highlighting, among other things, the importance of selecting an appropriate temporal scale when interpreting patterns caused by environmental variation.

Understanding bottlenose dolphin occupancy and habitat use patterns is advantageous for the efficient designation of marine protected areas and the regulation of human activities through marine spatial planning. For example, bottlenose dolphins have been found to change their behaviour and occupancy patterns in relation to boat traffic in Sarasota Bay, Florida (S. M. Nowacek, Wells, & Solow, 2001), while in the Moray Firth, Scotland, their foraging activity was reduced by 49% in the presence of vessels, with further reduction as boat traffic increased (Pirotta et al., 2015). Similarly, a 12-month acoustic study in the Spanish Mediterranean Sea found that recreational activities such as SCUBA diving and pleasure craft excursions impacted dolphin presence, with dolphins showing increased acoustic activity at times and seasons with lower human presence (Castellote et al., 2015). Knowing when animals are more likely to use an area based on environmental variables allows us to regulate human activities more efficiently, improving the protection of these populations. As our results highlight the site-specific habitat use patterns of these animals, it would be beneficial to investigate other areas along the coastline by deploying C-PODs in more locations. A more extensive passive acoustic monitoring scheme could further help delineate the seasonality of dolphin movements along the coast and possibly identify other important sites that have been overlooked thus far. This information can also be used as a basis for the design of mark-recapture abundance estimation surveys. Particularly for areas that pose high logistical obstacles for such studies (e.g., remote locations), knowing when dolphins are most likely to be present would maximise the likelihood of encountering them during targeted surveys, reducing both the cost and effort involved in monitoring this population.

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Chapter 4. Habitat use of a resident bottlenose dolphin population in the Shannon Estuary

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Author contributions:

1. Advice on model structure

ABSTRACT

The habitat preferences of marine mammals in coastal and estuarine environments may be affected by more fine-scale environmental variables than in offshore areas. However, in such areas, they may also face greater amounts of anthropogenic disturbance. This is particularly true for genetically and demographically isolated populations. In light of this, it is important to understand the habitat use patterns of cetaceans in such areas. A bottlenose dolphin population resident in the Shannon Estuary on the west coast of Ireland has long been monitored through abundance estimation surveys, as it is one of the qualifying features of a designated Special Area of Conservation (SAC). However, though two core areas of use within the estuary were previously identified, little has been done to identify the fine-scale habitat use patterns in the SAC. In this study, we used a long-term boat-based survey dataset spanning nearly two decades to model the habitat use of these bottlenose dolphins. Generalised additive models were implemented to model the presence of dolphins as a function of a suite of static and dynamic environmental and geographic covariates. Dolphin encounters peaked between June and August and in areas with north-facing slopes. Monthly variations in rainfall, chlorophyll *a*, and sea surface temperature did not show significant effects. The best performing models included a two-dimensional soap-film smoother of geographic coordinates and indicated that the location of dolphin occurrence depends on tidal state. A bottleneck region in the upper estuary appeared to be a prominent feature in the model outputs, likely due to the topographic effects on tidal current strength and direction. These results highlight the effect of fine-scale spatial and temporal features on bottlenose dolphin habitat use and how these should be taken into account in conservation and marine spatial planning.

4.1. INTRODUCTION

Mobile animals do not use the entire extent of their home range with the same intensity. In order to take advantage of patchily distributed resources, they develop patterns in their habitat use (Wiens, 1976). Understanding how and which environmental characteristics drive the habitat preferences of marine mammals can facilitate the development of appropriate conservation plans in order to protect them effectively. While some environmental variables appear to influence multiple species of marine megafauna in similar ways (e.g., attraction to frontal systems; Scales et al., 2014; Cox et al., 2018), intra-specific differences in habitat use are also apparent (e.g., harbour porpoises in some areas avoid high-flow tidal streams, while animals in other areas are attracted to them; (Benjamins et al., 2016), as are habitat- and location-specific responses to environmental predictors (see Chapters 2 and 3). Therefore, it is advisable to investigate habitat preferences on a population- or habitat-specific scale, rather than to generalise findings across an entire species' distribution range. This enables us to make more robust predictions of where animals occur, ultimately contributing to better management plans.

Bottlenose dolphins show high plasticity in their habitat use and foraging strategies (e.g., Pirotta et al., 2014; Fernandez-Betelu et al., 2019). Their habitat preferences can be driven by the type and concentration of prey available, as well as the presence or absence of competitors and predators, and their foraging behaviour adapts accordingly (Genov et al., 2019). Moreover, even within the same area, different lineages of dolphins are known to employ different feeding techniques, which may be passed down from mother to daughter, introducing a genetic and cultural dimension to habitat use (Sargeant, Mann, Berggren, & Krützen, 2005; Kopps et al., 2014). Social structure may also lead to habitat partitioning, as seen in the Shannon Estuary, Ireland. Here, within the same resident population, a small group of closely associated dolphins has been found to exclusively use the inner part of the estuary and a larger group with looser associations primarily uses the outer reaches of the estuary (Baker, O'Brien, McHugh, Ingram, & Berrow, 2018).

In Irish waters, genetic, demographic, and dietary evidence indicate that at least three distinct populations of bottlenose dolphins are present (Mirimin et al., 2011; Louis et al., 2014; Oudejans et al., 2015), namely, a resident population in the Shannon Estuary, a “mobile” population ranging along the west coast, and a “pelagic” population whose range extends beyond the continental shelf. The habitat preferences of the latter two were investigated and presented in Chapters 2 and 3, respectively. As an Annex II species in the

EU Habitats Directive, the estuarine bottlenose dolphin population is one of the qualifying species for which the Lower Shannon Estuary SAC was designated. In order to ensure that favourable conservation status of the population is maintained, abundance estimates have been calculated through boat-based surveys of the area for over a decade (Rogan et al. 2019). It is the most thoroughly studied of the three populations, with genetic (Nykänen et al., 2018), social structure (Baker et al., 2018), acoustic (Englund, 2014), and demographic (Englund, Ingram, & Rogan, 2007) analyses having been conducted over many years. The latest abundance survey was conducted in 2018, when there were an estimated 139 ± 15 animals in the population using the estuary (Rogan et al. 2019). Moreover, using data collected over a two-year period in the late 1990s, Ingram & Rogan (2002) identified two core areas of use within the estuary and found that dolphin presence correlated with deeper waters and steeper slopes. However, more detailed up-to-date information on the habitat preferences of this population, using a larger data set, is needed to ensure a fuller understanding of their movement patterns and to determine whether they are linked to seasonal or more fine-scale temporal changes, or influenced solely by static features of their environment. The Shannon Estuary is a hub of industrial and recreational activity, and it is well established that vessel traffic can have short- and long-term impacts on bottlenose dolphins (Bejder et al., 2006; Pirotta et al., 2015). Therefore, a more detailed understanding of their movements can help regulate vessel traffic in critical areas.

Long-term datasets are useful for population monitoring, because they allow us to detect changes and trends in the size and demography of the population. An additional benefit of large datasets is that they provide a more robust sample of observations on which to base habitat models. Models that rely on multiple years of data collection are better able to distinguish the processes underpinning habitat use patterns from noise in the dataset. They can also be used to assess temporal trends and interactions with dynamic variables, partitioning observations into various grouping levels (e.g., different seasons, years, tidal phases) while retaining a sufficient amount of data in each to allow robust statistical inference. The aims of this study were to investigate the habitat use of the resident bottlenose dolphin population in the Shannon Estuary, using the available long-term monitoring dataset, and to assess the influence of tides on the animals' distribution patterns, highlighting whether specific areas of the SAC require heightened protection.

4.2. METHODS

4.2.1. Study area

The Shannon Estuary is on the west coast of Ireland, where the River Shannon meets the Atlantic Ocean (Figure 4.1). It varies considerably in width and depth, being 2 km wide at its narrowest point and over 10 km wide at its mouth, approximately 50 m deep in its central channel, and featuring several shallow sandbanks, reefs, and mudflats. It is characterised by strong tidal currents (often $> 2 \text{ ms}^{-1}$) and has a maximum tidal range of approximately 5.4 m (Phoenix & Nash 2017). It is a major shipping lane, sheltering Ireland's premier deep-water port, and a hub of industrial activity, including an aluminium plant and two electricity generating power stations on its shores.

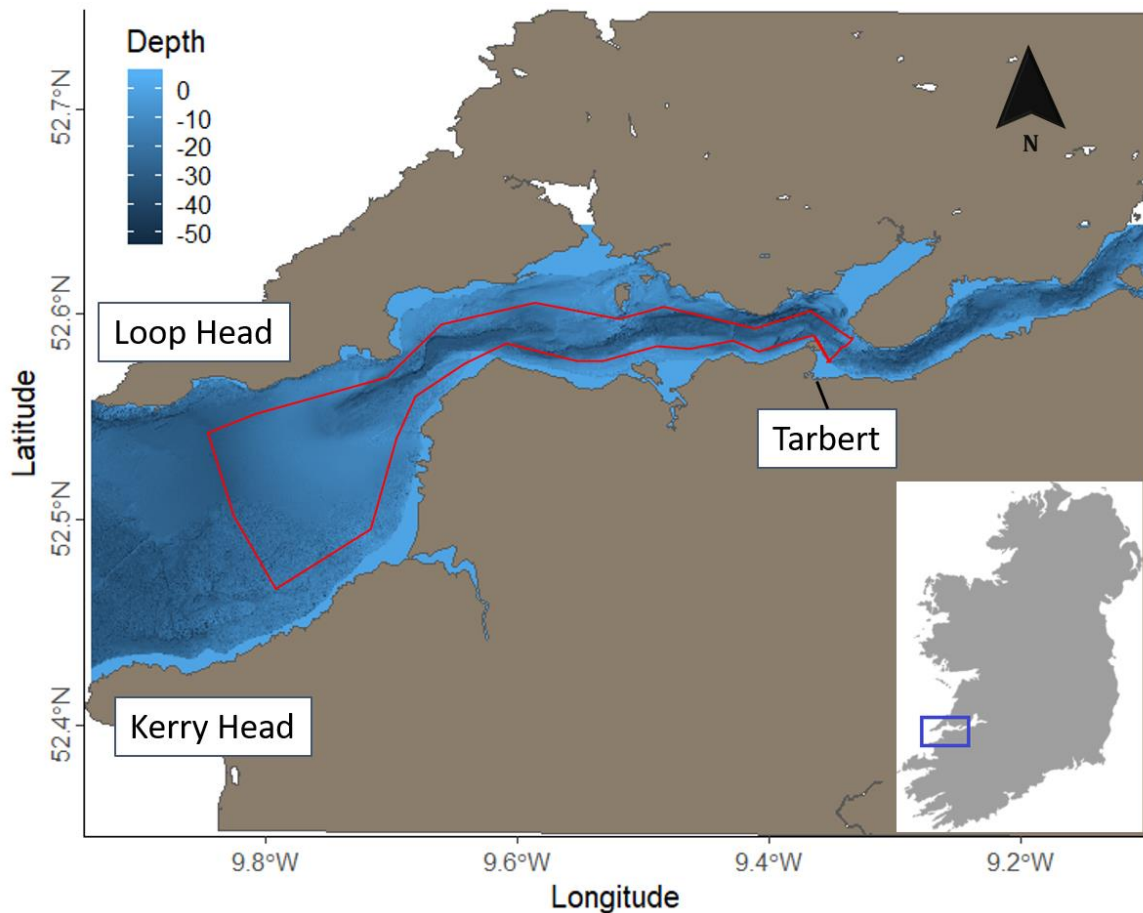


Figure 4.1. Map of the study area within the Shannon Estuary SAC. The SAC's westernmost boundary is the line between Loop Head and Kerry Head. Blue gradient shows the bathymetry (in m, from INFOMAR), red line denotes an indicative survey trackline. Surveys usually commenced at the port of Tarbert. Inset: map of Ireland showing the extent of the SAC (blue square).

4.2.2. Data collection and processing

Boat-based bottlenose dolphin surveys have been conducted in the lower estuary for over two decades (Ingram 2000; Englund et al 2008; Rogan et al. 2018). For the present study, we used data collected between 2001 and 2018 for which effort data were available. Surveys were undertaken from a Rigid hull Inflatable Boat (RIB) in Beaufort sea state <4, low swell, and good visibility conditions, allowing observers to detect dolphins up to 1 km or more from the vessel. Surveys took place primarily between the months of May and October, although winter surveys also occurred in some years. Transects usually covered a standard ~80 km long route, looping from one end of the study area to the other and back along the opposite shore within a single day (Figure 4.1). The GPS position of the boat was recorded at regular intervals (every five minutes in the earlier years, every minute in the later ones). Observers scanned the water on either side of the RIB until dolphins were sighted. The location, size, and composition (number of adults, calves, neonates) of the group was recorded and photographs were taken of the dorsal fin of each animal. Once all animals were photographed or contact with the group was lost, the survey was resumed. The number of animals in each group was estimated in the field and later corroborated through photo-identification. (A detailed description of the photo-identification process is given in Chapter 5).

4.2.3. Habitat models

The distribution of dolphins within the estuary both within and between years was modelled using a suite of environmental covariates using generalised additive models (GAMs). GAMs were run using the ‘mgcv’ package (Wood 2017) in R version 3.5.2 (R Core Team 2018). The study area was divided into 2 km x 2 km grid cells and both the response and predictor variables were aggregated to this resolution. I tested finer scale resolutions prior to selecting this one, but the large amount of zero counts in dolphin sightings caused severe overdispersion and lack of convergence. Given that good sighting conditions allowed the detection of dolphins up to at least 1 km away from either side of the boat, a 2 km scale reflects the scale of survey effort.

As there was a large proportion of cells with no dolphin sightings recorded in each month, using the number of animals or the number of encounters per cell per month as a response variable resulted in over-dispersed data and very poor fit with several different error

distributions. Therefore, a binomial distribution with a “logit” link function was used, with the presence/absence of dolphins in each cell per month as the response variable.

Environmental variables incorporated in the models were both static and dynamic. Static covariates included depth (from the INFOMAR data access portal, www.infomar.ie/data), seabed slope and aspect (calculated from the bathymetry data using the ‘raster’ package in R), and geographic coordinates (Universal Transverse Mercator coordinates of the centre of each grid cell; using UTM instead of latitude/longitude enables us to intuit the effect of this predictor as the distance in metres from a specific geographic feature). Dynamic covariates included monthly rainfall (in mm, from Met Éireann’s archival data portal, www.met.ie/climate/available-data/historical-data), sea surface temperature (SST, in °C) and chlorophyll *a* concentration (chl, in mg m⁻³). Due to the coastal/inland location of the study area, remotely sensed data were not available for most of the estuary. Therefore, SST and chl were downloaded from NASA’s SeaWiFS (for years prior to 2003) and MODIS Aqua (from 2003 onwards) satellite sensors as monthly averages of an 8 km x 8 km region just outside the mouth of the estuary. Survey effort was also allocated a four-level tidal state classification (Table 4.1). High and low water level predictions were generated for the port of Tarbert for the entire survey period using POLTIPS version 3.9.0/16 predictive software (National Oceanography Centre, UK). Days when high-tide water level exceeded 4.6 m and low-tide water level fell below 1.59 m were classed as spring tides, while all other days were classed as neap tides. The time intervals between each high tide and the succeeding low tide were classed as ebb tides, while intervals between each low tide and the following high tide were classed as flood tides. Each GPS point of survey effort was assigned to a spring/neap category, depending on the date of the survey, and to an ebb/flood category, depending on which interval it occurred in. These categories were then combined into one classification (e.g., spring ebb, neap flood, etc.), so that during a single day it was possible for effort to be classed as spring flood at the start of the survey (if it started after low tide) and spring ebb after the tide turned.

Table 4.1. The four tidal state categories, showing how each level was computed: spring and neap tides were based on predicted high and low water levels above chart datum, while ebb and flood tides were based on the predicted times of high and low water each day (NOC UK).

	Neap Low tide > 1.6 m High tide < 4.59 m	Spring Low tide < 1.59 m High tide > 4.6 m
Ebb From high to next low tide	Neap Ebb	Spring Ebb
Flood From low to next high tide	Neap Flood	Spring Flood

To account for any biases in the distribution of survey effort, an offset was calculated for each grid cell per month and per tidal state. The offset was equal to the sum of the length of survey tracklines crossing the cell during each of the four tidal state categories in each month. The logged offset term was included in each of the models described below.

The covariates were tested for collinearity using Variance Inflation Factors (VIF) and only included in the models together when their VIF was < 3. As depth showed considerable collinearity with longitude, two sets of GAMs were run on the dataset, a “bathymetric” one and a “geographic” one. The bathymetric models included depth and all the other covariates except coordinates, while the geographic one included a two-dimensional coordinate spline and all the other covariates but depth. A penalised thin-plate spline (“ts”) was used with all covariates except aspect and latitude-longitude coordinates, allowing each variable’s smoother to shrink to zero if it did not contribute to the model in any meaningful way (Wood 2003). As aspect is a cyclical term, i.e., both 0° and 360° slopes face north, a cyclical cubic spline (“cc”) was used for that variable. A soap-film smoother was used in the two-dimensional spline (“so”) to incorporate the shoreline and prevent predictions from “spilling” across land barriers. The knots used to create this soap-film were placed at equidistant points 2 km apart, as Wood, Bravington, & Hedley (2008) caution that they should not be spaced at a coarser resolution than our observations and a finer grid resulted in prohibitively slow computation time. For both sets of models, the initial ones contained all the covariates and an interaction with the tidal state factor. Variables were dropped from the models if their smoothers shrank to zero or they were not significant, until only significant predictors were retained. In each set of models, the first model was run on the entire dataset, while the second was run using only data from May–October. (For other model setups that were tested, see Appendix IA). Each pair of

equivalent bathymetric and geographic models was compared using Akaike's Information Criterion (AIC) to select the best fitting one.

4.3. RESULTS

A total of 119 surveys were conducted during the years 2001–2003, 2005–2008, 2015, and 2018, resulting in 428 encounters with bottlenose dolphins. Most surveys took place during spring tides but the highest number of encounters was observed in neap flood tides (Table 4.2).

Table 4.2. Amount of survey effort that took place and number of encounters with bottlenose dolphins in each tidal state during 119 boat-based surveys of the Shannon Estuary.

	Survey effort (km)	Number of encounters
Neap Ebb	1629.6	47
Neap Flood	1629.5	170
Spring Ebb	3960.4	105
Spring Flood	4231.3	124

4.3.1. Model results

Model diagnostics and AIC showed that the geographic model was a better fit to the data than the bathymetric model in all scenarios (Table 4.3). When modelling the entire dataset, the bathymetric model retained aspect and slope as significant variables in at least one tidal state (aspect during all spring tides, $P < 0.030$, and slope during spring ebb tides, $P = 0.006$), while the geographic model retained coordinates and month as significant predictors ($P < 0.020$). When modelling the summer (May–October) data only, aspect was retained in both models during spring flood tides ($P = 0.03$ and $P = 0.01$, respectively); depth was significant during spring ebb tides ($P = 0.007$) and geographic location was significant on all levels ($P < 0.001$) except neap flood tides. While the geographic summer model explained only 7.47% of the deviance observed, this was a higher percentage than was explained by any of the other models.

The best-performing models (namely, the geographic ones) showed that year-round dolphin presence peaked between June and August ($P = 0.012$) (Figure 4.2) and was significantly associated with north-facing slopes (0° and 360°) during the summer ($P = 0.010$) (Figure 4.3). The two-dimensional smoothers for both the entire dataset and

the summer only dataset showed very similar patterns (Appendix IIC and Figure 4.4). During ebb tides, predicted dolphin presence was concentrated west of the narrowest point of the estuary, while during flood tides, the location with the highest probability of encounters was further west. In neap flood tides, dolphin presence was restricted to the outer part of the estuary, while in spring floods, animals were also found along the southern shore of the inner estuary. In all tidal states, dolphins were not predicted near the north shore of the inner estuary. (For comparison of predicted and observed dolphin sightings see Appendix IIC).

Table 4.3. Covariates retained as significant predictors, AIC values, and deviance explained by each model. Entire dataset: observations from all months. Summer dataset: data collected between May–October of every year.

	Bathymetric model			Two-dimensional model		
	Covariates	AIC	Deviance explained	Covariates	AIC	Deviance explained
Entire dataset	Slope, aspect	1708.808	2.92%	Coordinates, Month	1666.826	6.91%
Summer dataset	depth, aspect	1495.251	3.62%	Coordinates, aspect	1481.666	7.47%

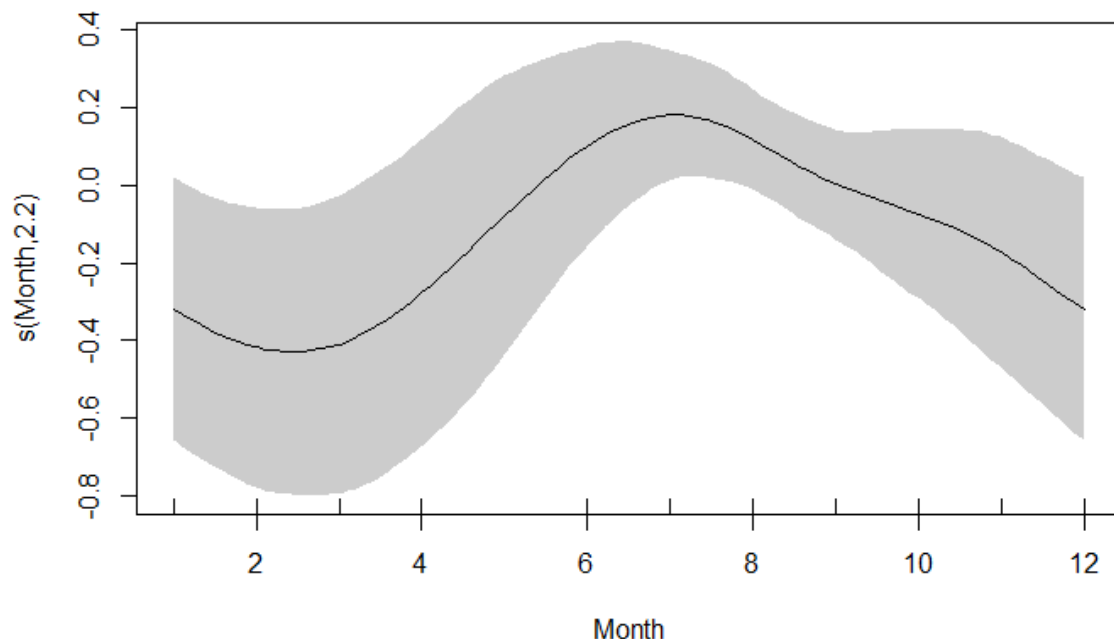


Figure 4.2. Estimated smoothing curve of bottlenose dolphin presence throughout the year (Month 1 is January, 12 is December), in all tidal states. Solid line is the smoother, rugs on the x-axis denote observed covariate values, shaded region indicates 95% confidence intervals. Y-axis shows strength of the effect of the covariate on dolphin presence, with estimated degrees of freedom in brackets.

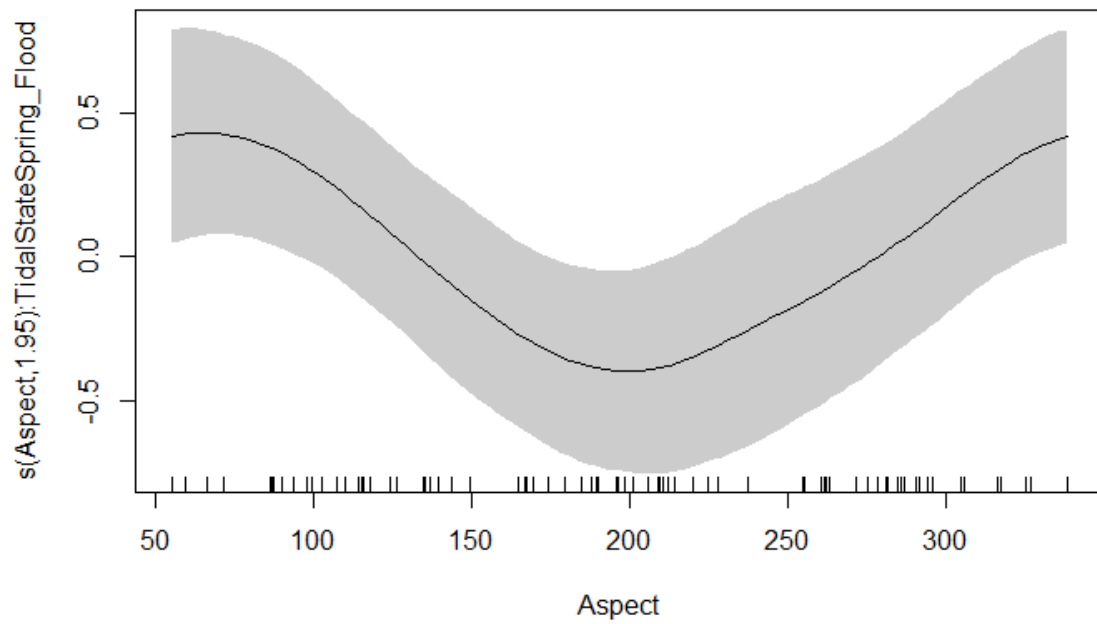


Figure 4.3. Estimated smoothing curve of the relationship between bottlenose dolphin presence and seabed aspect during spring flood tides in summer months (May to October). Solid line is the smoother, rugs on the x-axis denote observed covariate values, shaded region indicates 95% confidence intervals. Y-axis shows strength of the effect of the covariate on dolphin presence, with estimated degrees of freedom in brackets.

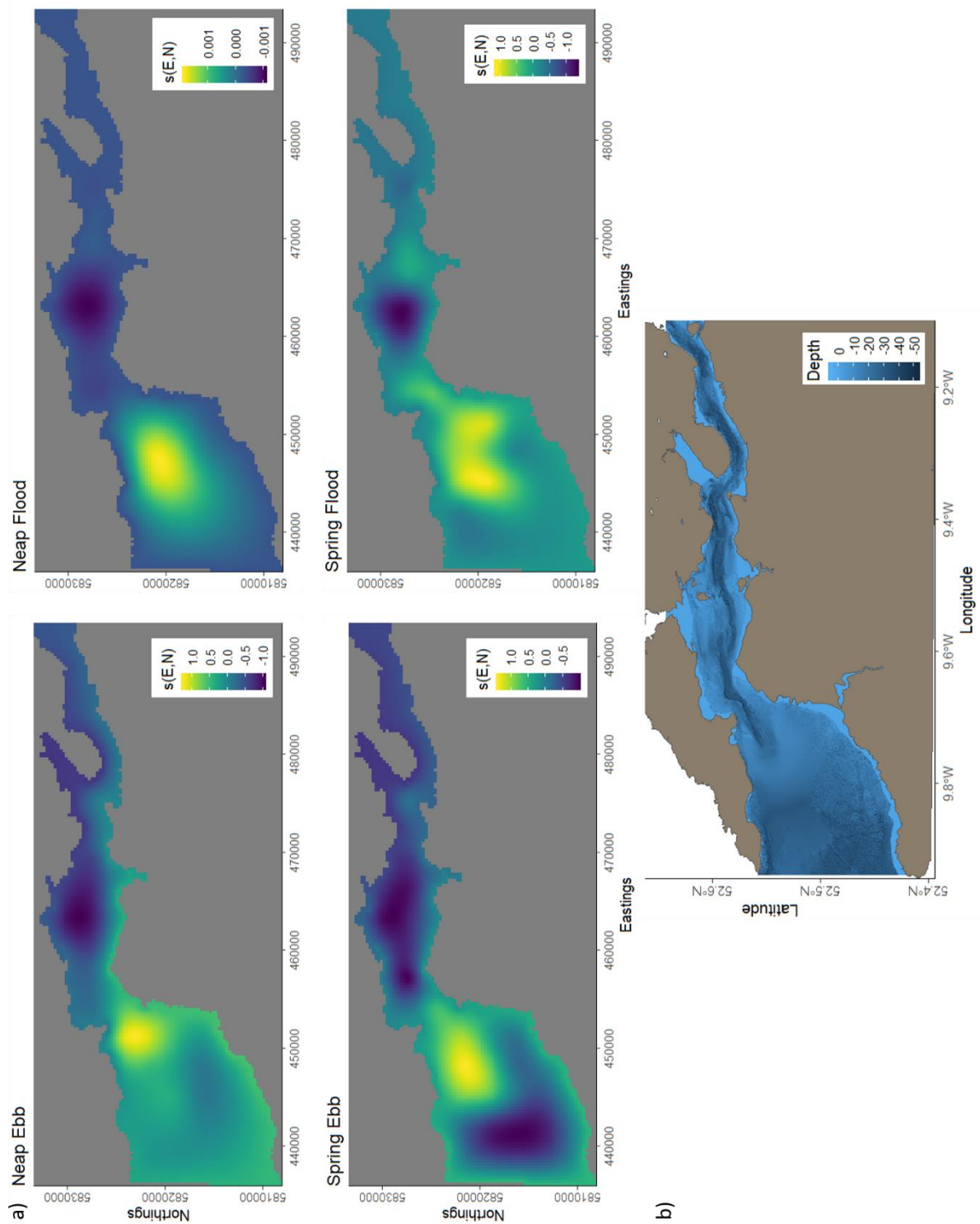


Figure 4.4. a) Presence of bottlenose dolphins modelled as a two-dimensional smooth function of geographic coordinates within the study area during each of the four tidal states. Colour scale reflects strength of the effect, not predicted probability of presence. b) Bathymetry of the study area; colour gradient shows depth in metres (from INFOMAR).

4.4. DISCUSSION

In the present study, I modelled the habitat use patterns of a resident population of bottlenose dolphins in an estuarine SAC on the west coast of Ireland, using a long-term boat-based survey dataset. Suitable data that could be weighted by survey effort were available for nine separate years, spanning nearly two decades. As outlined in previous chapters, understanding the habitat preferences of marine mammals provides useful information for the better design and implementation of effective spatial planning, monitoring, and conservation strategies.

Seabed aspect was retained as a significant predictor of dolphin presence in most of the models, specifically indicating an affinity with north-facing slopes to be important during spring flood tides. The geographic models predicted a higher probability of dolphin presence along the south shore of the inner estuary during spring flood tides than at any other tidal state. Therefore, the link with north-facing slopes may have to do with the orientation of the shoreline and deep-water channel within the estuary, rather than aspect per se having a causal effect on dolphin distribution throughout the area. To elaborate further, dolphins have been observed foraging, milling, and socialising around and above two large sandbanks in the outer estuary, the Kilstiffin and Ballybunion Banks (MG, unpublished data), so it is unlikely that the orientation of those slopes per se affects dolphin distribution. A detailed spatio-temporal analysis of their specific behaviours around these features would elucidate whether they do, in fact, use different aspects for different purposes. Sandbanks are known to act as fish nurseries (Kaiser et al., 2004; Ellis et al., 2011), which would make these locations attractive foraging areas, especially coupled with the fact that dolphins can utilise the seabed to corral fish toward shallower water and trap them more easily. While sediment sampling of these two sandbanks has shown them to host at least 81 infaunal and benthic invertebrate species (Aqua-Fact Intl Services Ltd. 2007), the precise composition and distribution of fish in the water column around them has not been investigated. Such information would be useful in understanding the ways dolphins use these fine-scale habitats.

Bottlenose dolphin presence in the study area was highest during June–August. Abundance estimates have indicated that fewer dolphins are found within the SAC in winter than in summer months (Englund et al., 2007). Members of this population have been sighted in neighbouring bays outside the estuary (Levesque et al., 2016) but the exact geographic boundaries of this population's range are not known. The lower numbers

within the SAC during winter could result from the animals dispersing over a wider region in pursuit of prey that is affected by seasonal fluctuations in temperature. While association of bottlenose dolphins with warmer temperatures has been found elsewhere (see Chapters 2 and 3), as this population does not completely abandon the estuary even in the coldest months, it is unlikely that the surface temperature changes in this area directly affect the dolphins themselves. Similar lower sighting rates during cold seasons were also found in a population of Guiana dolphins (*Sotalia guianensis*), suggestive of wider dispersal in search of prey (Daura-Jorge et al., 2005). In addition to this, the Shannon is an important salmon (*Salmo salar*) river and dolphins have often been observed chasing and tossing these fish in the study area. The higher likelihood of dolphin sightings during June–August suggests that this is an important foraging area during the salmon run. Associations with migrating salmon were also observed in the Moray Firth by Pirotta et al., (2014) and salmon is a known valuable food source for this top predator (Janik, 2000). In addition to this, the Shannon Estuary is an important calving area, with neonates appearing from mid-to-late June to August (Ingram, 2000; Englund, 2014; Baker et al. 2018; Rogan et al. 2019; MG, unpublished data). The absence of predators, such as sharks (Heithaus, 2001), from the estuary likely makes it a safer calving and nursery area than the waters beyond it.

Overall, the models performed quite poorly in terms of explaining the observed deviance in the data. This may be attributed to the inability of the variables included in the models to sufficiently describe the underlying drivers of the dolphins' movement patterns. Bottlenose dolphins are highly adaptive in their habitat use, occupying a range of different environments and adopting various foraging strategies; this makes modelling their habitat preferences a challenge, as their response to different environmental variables can be highly habitat-specific (see Chapter 2). Another reason for the underperformance of the models could be the spatial resolution of the bathymetric variables used. In the relatively small confines of the study area, it is possible that fine-scale topographical features have a much more direct influence on dolphin movements and behaviour than, for instance, the overall primary productivity or surface temperature of the region. Unfortunately, the scale selected was the finest at which models could be implemented and, even so, the large number of zeros in the resulting dataset presumably also contributed to poor model fit. While a coarser scale could have been used to minimise this latter issue, the features of the seabed would have been even further obscured if aggregated to a larger grid cell size; thus,

a considerable amount of the environmental variation would have been lost, rendering the influence of bathymetric covariates even less informative.

The spatial resolution issue described could further explain why the bathymetric models consistently explained less of the observed deviance than the geographic models. Relatively small features such as sandbanks and reefs can play a considerable role in influencing prey aggregations; when averaged across the relatively large grid cells we used, the resulting benthic topography is more homogeneous compared to reality. While Ingram & Rogan (2002) found that bottlenose dolphins in the estuary were encountered predominantly in deeper waters and over steeper slopes, their analysis used a 1 km x 1 km grid resolution. The geographic model in the present study was better than the bathymetric one at reflecting the distribution of dolphins based on their location relative to topographic features, rather than on the features themselves. A key feature in this area appears to be the bottleneck area located between Leck Point (Co. Kerry) and Kilcredaun Point (Co. Clare) between the inner and outer parts of the estuary, in keeping with the findings of Ingram & Rogan (2002). Current velocities in this area vary considerably depending on the phase of the tide, often exceeding 2 ms^{-1} during spring ebb tides, albeit slightly weaker during flood tides (Cox, 2015). The combination of these strong currents rushing through the deep-water channel in the middle of the estuary, a shallow sandbank, and a sharp change in the angle of the southern shoreline, creates predictable hydrographic features that could drive prey aggregations or serve as barriers against which to trap fish (Hastie et al., 2004; Bailey & Thompson, 2010). Specifically, not only is the turbulence of the water increased by strong currents, but the different water velocities described create persistent downwelling features during part of the tidal cycle (Cox, 2015). Up- and downwelling currents are known to aggregate plankton as it moves passively in the water column (O'Boyle & Silke, 2010) and this could attract animals of higher trophic levels. Further, as adult salmon move upriver (Aprahamian, Jones, & Gough, 1998) and smolts remain in place during flood tides (Lacroix & McCurdy, 1996), this could explain why the probability of sighting dolphins in the inner part of the estuary increased during spring flood tides; the smaller change in water levels during neap tides presumably plays a lesser role in fish movement, and thus neap flood tides do not have the same effect on dolphin presence upriver.

The predicted absence of dolphins from the northern side of the inner estuary, regardless of tidal state, emerged as a consistent pattern from the two-dimensional models. This area

shows small bathymetric variation, so it is possible that the lack of prominent topographical features leads to fewer or smaller prey aggregations than elsewhere in the study area. This would make it a less attractive foraging spot compared to the bottleneck area and sandbanks further west, or to the narrow channel at the eastern end of the study area, where strong tidal currents are also observed. The infrequent sightings of dolphins on the north shore of the inner estuary does not necessarily preclude their use of the area, however. Animals that have been sighted there have been observed moving slowly and non-directionally, doing long dives, or showing evasive behaviour towards dolphin-watching boats (MG, unpublished data). If the dolphins prefer to rest in these slower water currents, their lower mobility might render them harder to detect from a survey platform than groups of travelling or foraging dolphins. Moreover, if disturbed by a research vessel while resting, their subsequent evasive behaviour would make it difficult to record precise encounter data. All these factors could result in lower detection rates in this vicinity, but do not clearly imply that the area is not used by dolphins.

As is common in estuarine environments (Warwick et al., 1991; Mao et al., 2004;) our results reflect a strong interplay between static and dynamic features. Tide is clearly an important driver of dolphin movements around the estuary. Predictable hydrographic features can play as strong a role as static topographical ones; indeed, the core areas identified by Ingram & Rogan in 2002 remain prominently in use even with data spanning an additional 15 years. Bottlenose dolphins are highly flexible in their prey choice; although there are still considerable gaps in our knowledge about their feeding preferences in Irish waters, we do know that they feed on salmon in the Shannon Estuary (pers. obs.). Furthermore, Hernandez-Milian et al. (2015) found evidence that gadoids, such as pollock (*Pollachius* spp.), flatfish, such as dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*), mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), and even conger eels (*Conger conger*) form part of bottlenose dolphin diet. All of these species are found within the Shannon Estuary, as are high numbers of sprat (*Sprattus sprattus*), which attract larger predators (Central & Regional Fisheries Boards, 2008). It would be useful to study the temporal changes in the abundance of species from lower trophic levels, both at broad and fine scales. For instance, quantifying the seasonal changes in abundance of fish species in the SAC and surrounding coastal waters could be helpful in defining the reasons behind the seasonality in dolphin presence. Finer-scale studies of the movement of plankton and smaller fry in the water column and the potential aggregation of larger prey items around dolphin preferred areas would help testing our hypothesis that the

dolphins in this area use specific hydrographic, as well as topographic, features to augment their foraging. More in-depth studies of how the dolphins move in the water column would also shed light on how they chase or trap their prey. As the sub-surface visibility conditions in the estuary are generally too poor for video-imaging methods to be effective, a suitable alternative could be the use of multibeam sonar methods, which have been used to study the foraging techniques and prey manoeuvres of killer whales (*Orcinus orca*) and bottlenose dolphins (Ridolix et al., 1997; Similä, 1997; Nøttestad & Axelsen, 1999).

This population of bottlenose dolphins is protected not only as an Annex II species of the EU Habitats Directive, but also as an indicator species of the condition of the Shannon Estuary SAC. As such, it is monitored through abundance estimate surveys to ensure that the population size remains stable (see Chapter 5). However, merely monitoring population size is not enough for its adequate protection and management, if we do not understand the drivers behind the animals' movements. It is known that these dolphins do not remain within the official boundaries of the SAC, nor is their abundance consistent year-round; such patterns have also been observed in the Moray Firth, Scotland, and have implications regarding the effectiveness of area-based management (Wilson et al., 2004; Arso Civil et al., 2019). Knowing which environmental factors attract dolphins to specific areas and understanding the underlying processes determining their habitat use patterns would enable us to a) identify areas of higher use during specific times and whether these areas need stricter protective measures than the rest of the SAC and b) further investigate the ranging patterns of these animals outside the estuary in a more targeted fashion, by surveying areas that may fulfil similar conditions. Vessel traffic has been shown to alter bottlenose dolphin behaviour in other areas (Pirotta et al., 2015), as well as lead to long-term declines in abundance (Bejder et al., 2006). This estuary is a major shipping channel, as well as a hub of tourist activity; therefore, it may be critical to identify the role specific estuarine features play in bottlenose dolphin movement in order to mitigate the potentially harmful effects of boats in their vicinity.

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APPENDIX IIA

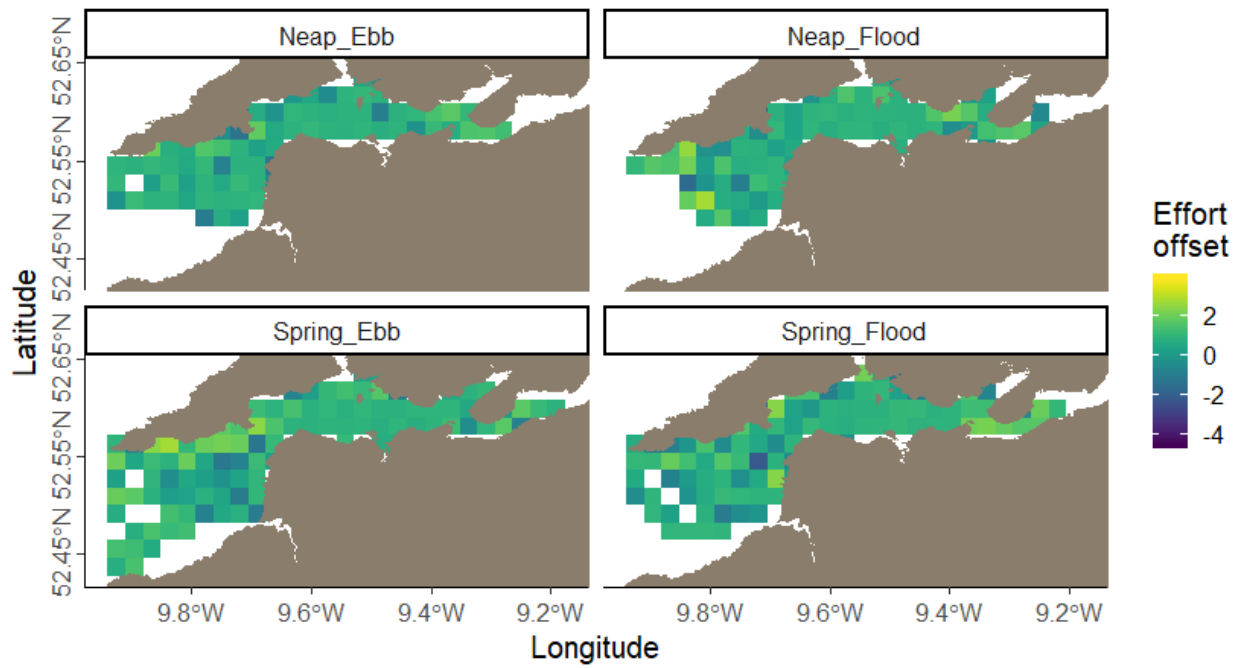


Figure IIA.1. Offset values per grid cell used to account for spatial bias in survey effort, for each of the four tidal states used in the models. The offset for each cell is equal to the log of the summed length of track lines traversing the cell. Within the models, these values were calculated for each month separately.

APPENDIX IIB

Alternative GAM setups that were considered to model bottlenose dolphin habitat use in the Shannon Estuary, but were either computationally prohibitive or did not converge due to lack of observations or overdispersion.

Using first all data and then April–October data:

- A) Number of encounters against all static and dynamic covariates using a:
 - a. Poisson distribution
 - b. Quasi-Poisson distribution
 - c. Tweedie distribution
- B) Presence of dolphins against all static covariates including an interaction with Year
- C) Presence of dolphins against Latitude and Longitude including an interaction with Year
- D) Presence of dolphins against all static covariates including an interaction with Month
- E) Presence of dolphins against Latitude and Longitude including an interaction with Month

Using November–March data:

- A) Presence of dolphins against all static and dynamic covariates including a Tidal State interaction
- B) Presence of dolphins against Latitude, Longitude, and dynamic covariates, including a Tidal State interaction

APPENDIX IIC

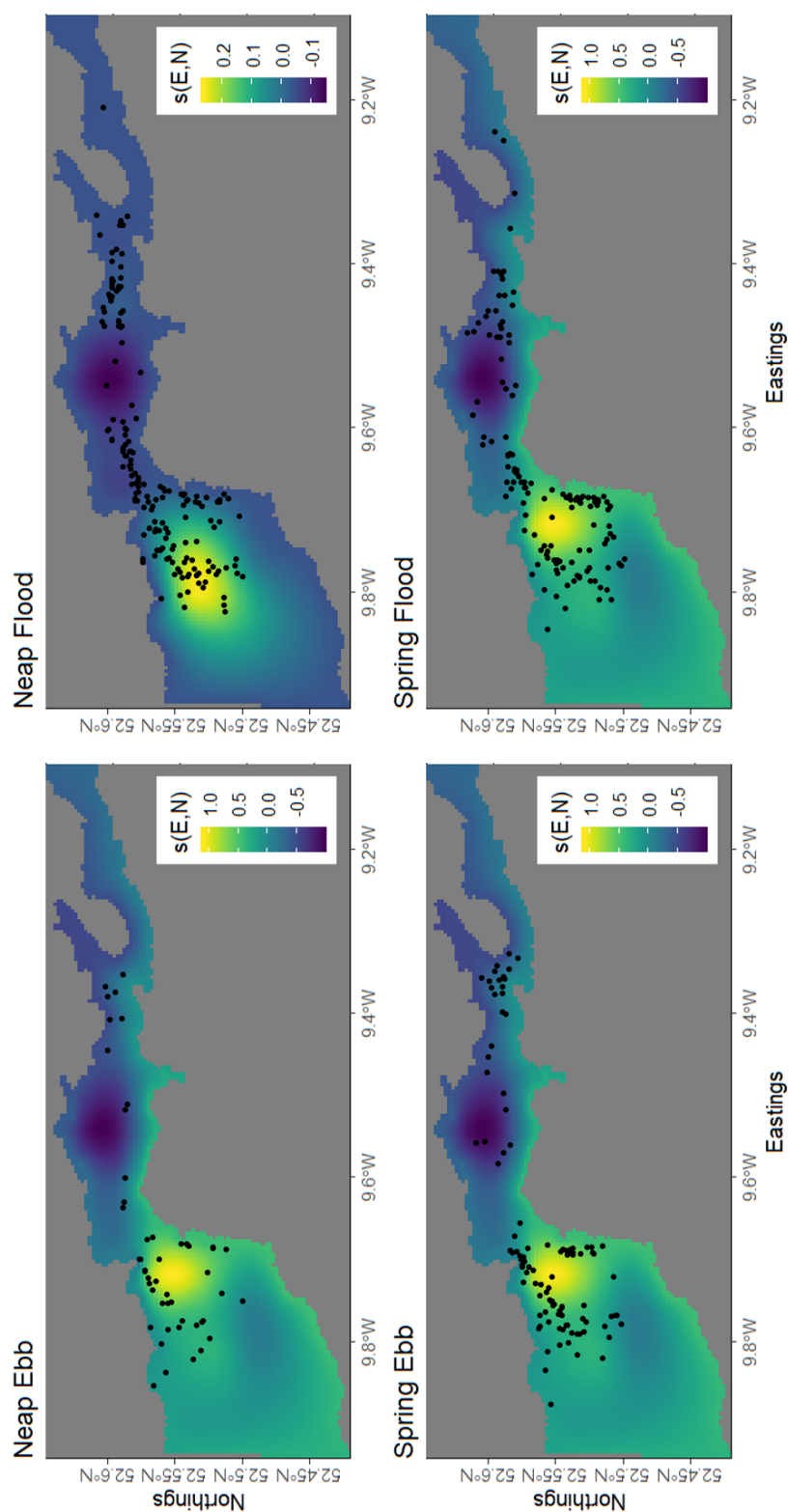


Figure IIC.1. Estimated bottlenose dolphin occurrence in the Shannon Estuary plotted as a two-dimensional soap film smoother of geographic coordinates, using data from all months within each year. Colour indicates strength of the effect on sighting probability. Dots indicate observed dolphin sightings.

Chapter 5. Using mark-recapture data collected from an ecotourism vessel to monitor a resident bottlenose dolphin population

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Author contributions:

1. Photo-ID and abundance estimation for 2015 dataset

ABSTRACT

Precise and accurate abundance estimates are fundamental to successful conservation monitoring of cetacean populations. Standardised mark-recapture surveys are typically used to monitor bottlenose dolphins within protected areas. However, since these surveys can be logistically and financially cumbersome where funding is lacking or there are competing priorities, monitoring commitments beyond the minimum statutory requirements are not common practice. Standardised surveys of a resident bottlenose dolphin population using a protected area in western Ireland are conducted in compliance with monitoring obligations. However, their infrequent occurrence provides only limited power to detect changes in population size. Here, the potential of using mark-recapture data collected from a dolphin-watching vessel was investigated as a cost-effective method to augment population estimates derived from these infrequent dedicated surveys. Estimates derived using data collected from each method and the effort required to collect sufficient data were compared. The effect of spatial bias resulting from the use of such a platform of opportunity (POP) to collect mark-recapture data was also examined. Using photo-identification data and a closed population model in both cases, the standardised method used in 2015 and POP survey data collected in 2016 returned similar estimates of 114 ± 13.5 (SE) and 107 ± 8 (SE) dolphins, respectively. Unevenly distributed effort and the limited range of the POP meant that more time on the water was required to generate an estimate with an equivalent precision to that of standardised surveys. Use of POP data offers many cost-effective additional benefits to long-term monitoring. Besides increasing the likelihood of detecting changes in population size in a timely fashion, it can provide detailed demographic data, and enables individuals within the population to be tracked on an annual basis.

5.1. INTRODUCTION

Monitoring the status (overall health, abundance, and reproductive capacity) of a cetacean population is fundamental to the successful implementation of a conservation management plan (Taylor et al., 2007; Wilson, Hammond, & Thompson, 1999). The methods employed to calculate cetacean abundance are diverse, but an often-used method involves visual surveys from an aerial, land-, or boat-based platform (Evans & Hammond, 2004). Sampling design and survey effort depend on whether monitoring is based on the density of animals within the area, or on absolute numbers in the population. For instance, large-scale transect surveys aiming to calculate the density of marine megafauna in the area surveyed (Hammond et al., 2013; Macleod et al., 2009; Rogan et al., 2017, Chapter 2) require evenly distributed survey effort and equal coverage probability design. Conversely, to determine the absolute number of animals using a study area, techniques such as mark-recapture are used, for which emphasis is placed on gaining a representative sample of individuals and maximising sighting rates (Hammond, 2010) rather than habitat coverage.

Mark-recapture is a commonly used method to estimate the absolute abundance of a population when animals can be individually marked and therefore identified (Otis et al., 1978). In the case of some cetacean species, the ability to identify individuals using photographs of their natural markings circumvents the need to physically capture and tag each animal (Hammond, 1986; Markowitz, Harlin, & Wursig, 2003). For bottlenose dolphins (*Tursiops* spp.), these identifiable markings consist of nicks, notches, and rakes along the dorsal fin and flanks; these scars are acquired through interactions with conspecifics, predators, vessels, or fishing gear (Lockyer & Morris, 1990; Luksenburg, 2014). Although such markings can change over time, they usually remain readily identifiable within the relatively short period of a single survey season (Hammond, 1990; Williams, Dawson, & Slooten, 1993). Moreover, if a dolphin population is surveyed frequently, these changes may be tracked between years and their rate of change calculated. In this way, a single individual that may acquire new nicks and notches remains recognisable and is not mis-identified as a new one, despite cumulative major changes in the appearance of its dorsal fin over several years (Lockyer & Morris, 1990; Urian et al., 2015).

The frequency of dedicated photo-identification monitoring surveys often depends on the size of the area of interest and the home range of the population (Taylor et al., 2007), but,

despite the apparent rarity of actual datasets with sufficient power to promptly detect a decline (Taylor et al. 2007, Thompson et al. 2000), they should be regular enough to detect changes in a population in a timely fashion. This is especially critical for smaller or isolated populations, in which any decline in numbers increases the risk of local extinction (Keller & Waller, 2002; Valsecchi et al., 2004); timely responses in management practice are reliant on a prompt detection of a decline. Moreover, merely knowing the number of animals present in an area is not sufficient to provide adequate protection for the population. Of equal importance is information on its demographic parameters and changes therein, the health and reproductive status of its individuals, and how these factors influence their habitat use. For example, differences in sex- and age-specific survival rates were found in bottlenose dolphins in southern Brazil (Fruet et al., 2015), while Pack et al. (2017) found that the habitat use of humpback whale mother-calf pairs in Hawaii changed depending on the age and size of the calf. Knowing about these variations can inform protection and management plans, which can be tailored to target specific areas if it is known they are critical for particularly vulnerable population classes. However, a serious drawback of dedicated boat-based surveys of marine megafauna is the associated expense (Williams, Hedley, & Hammond, 2006; Taylor et al., 2007), especially in countries with limited funding for environmental monitoring or where there are competing priorities. There are also logistical constraints if the surveys are in remote or hard to access areas, and if there are limited trained researchers available. This often results in monitoring efforts meeting the bare minimum of requirements, both in frequency and detail of reporting.

One way to mitigate the cost of dedicated cetacean surveys is to use a platform of opportunity (POP) for data collection, i.e., a vessel that is deployed for some other reason besides the survey itself (Compton et al. 2007; Hauser et al., 2006; Kiszka et al., 2007; Williams et al., 2006). For example, ferries or whale-watching boats can be used to survey an area, often repeatedly, at a very low cost. However, the researchers rarely, if ever, have control over the movement of the vessel, meaning that the area surveyed is restricted by the purpose of the platform, as is the duration and the frequency of surveys. For instance, ferries that only operate between two points cover a mere fraction of a population's range; ecotourism boats tend to spend time in areas as close as possible to their launch point to minimise fuel consumption, and their operation is dictated by seasonal and daily demand. The spatial biases introduced by the use of POPs can lead to skewed detection probabilities or limited sample sizes, which can impact the results if not accounted for with appropriate

analyses. However, these limitations are often balanced by the need for information on the density of a cetacean population, or even of multiple cetacean species that occur in a given area, which would otherwise be very costly to obtain. POPs have successfully been used to answer a range of questions on a variety of species; from habitat use in whales (Ingram et al., 2007; Macleod et al., 2004) to inter-annual changes in occurrence in multiple odontocete species (Macleod, Brereton, & Martin, 2009), they provide key baseline information that can be built on for conservation purposes.

The common bottlenose dolphin (*Tursiops truncatus*) is a cosmopolitan species (Leatherwood & Reeves, 1990) listed in Annex II of the EU Habitats Directive. As such, EU member states are required to designate Special Areas of Conservation (SACs) and periodically report on their conservation condition. The lower Shannon Estuary (Figure 5.1) in western Ireland is one of two SACs in Irish waters with bottlenose dolphins as a qualifying feature. This population is genetically and demographically distinct from other bottlenose dolphin populations (Mirimin et al., 2011; Nykänen et al., 2018). Occasional dedicated monitoring surveys have estimated the population size to be between 107 ± 12 (SE) and 140 ± 12 (SE) individuals (Berrow et al., 2010; Rogan et al., 2018), and as such it is considered stable (Figure 5.2).

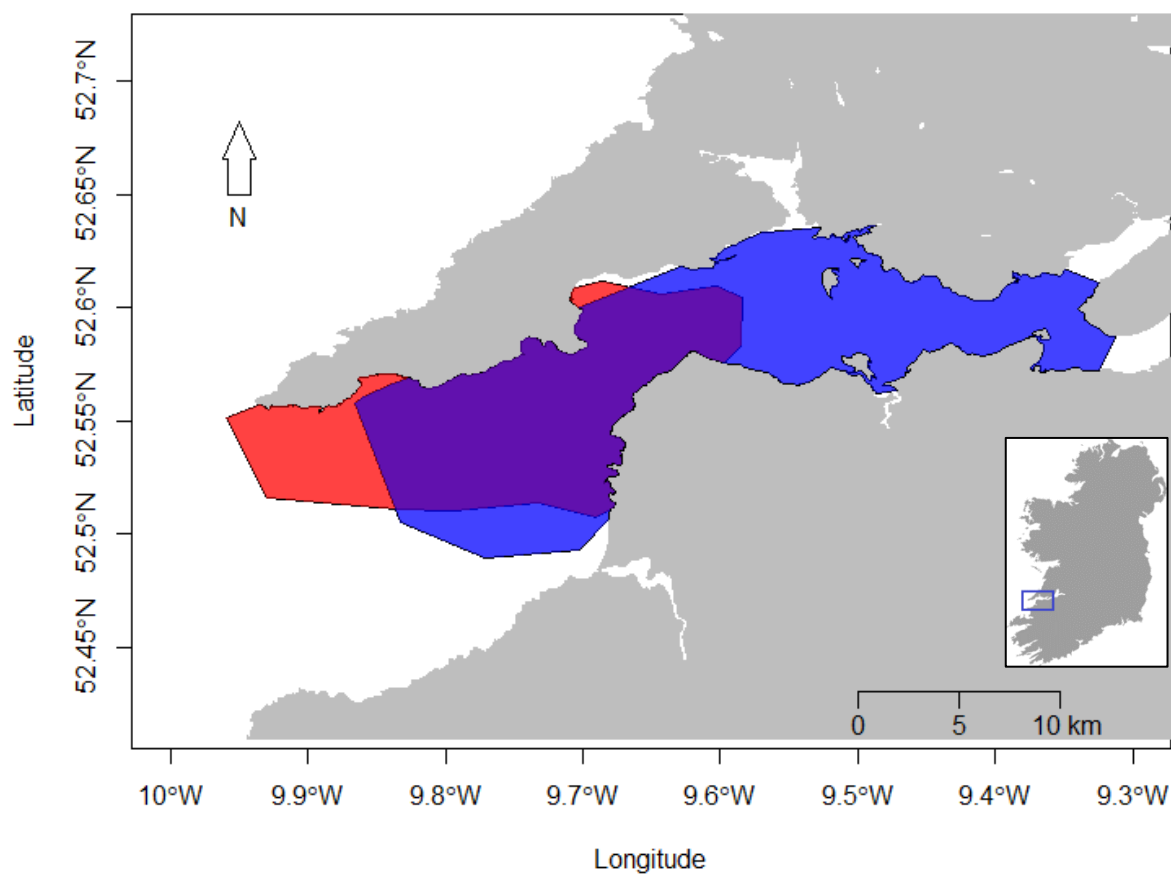


Figure 5.1. Map of the Shannon Estuary SAC showing the extent of the survey effort during dedicated monitoring surveys in 2015 (blue), the area covered by the dolphin-watching vessel in 2016 (red), and the overlap of these (purple). Inset: Location of the SAC on the west coast of Ireland.

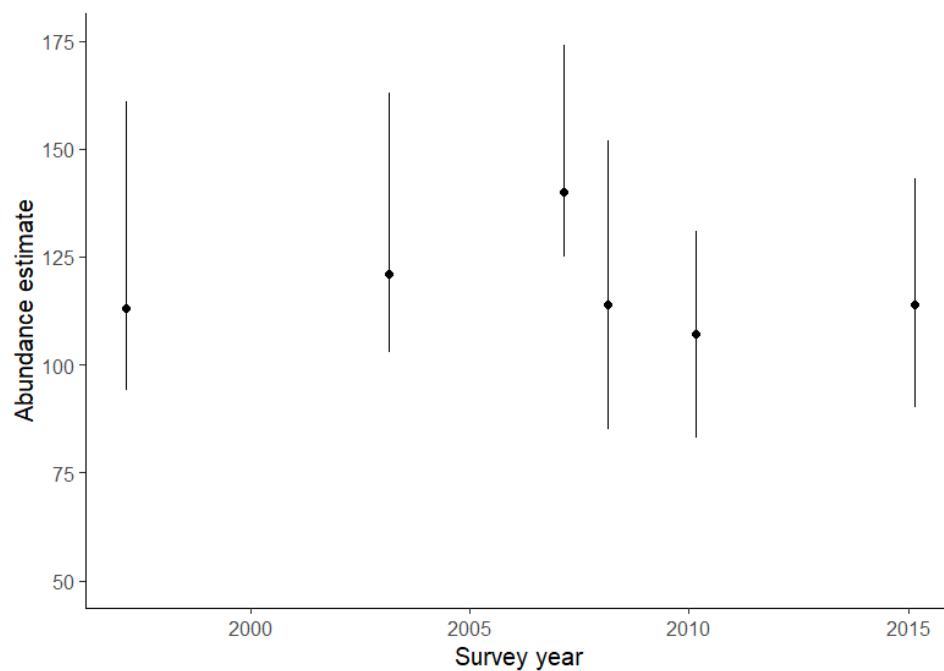


Figure 5.2. Abundance estimates and associated 95% confidence intervals generated from standardised surveys of the bottlenose dolphin population in the Shannon Estuary. Note the irregularity with which surveys took place.

Whilst providing precise estimates of abundance during the years in which surveys are commissioned, the irregular intervals between standardised surveys provide insufficient power to detect even dramatic declines in population within a short time frame, hence delaying any potential mitigating management response. A previous study on this population (Englund et al., 2007) showed that a 5% per year decline in dolphin numbers cannot be detected until 14 years have elapsed, by which time the population will have decreased by over 50%. Dedicated surveys of this population are relatively expensive and, despite the advantages offered by more frequent surveys, conservation authorities are often reluctant to fund survey effort beyond the basic level required for statutory reporting. Therefore, the present study examines the feasibility of using a dolphin-watching vessel as a POP that could be used as an interim survey tool between these more standardised surveys.

More specifically, the aim of this study was to investigate the potential for using mark-recapture photo-ID data collected from a POP to generate abundance estimates of sufficient accuracy and precision to provide valuable monitoring data, in order to augment infrequent standardised reporting surveys. Photo-identification and effort data were collected from a commercial dolphin-watching vessel and the results were compared to those of a dedicated survey conducted in the previous year. Potential sources of bias in the use of POPs were examined and ways to overcome them investigated.

5.2. METHODS

5.2.1. Study area

The Shannon Estuary is at the mouth of Ireland's longest river, the River Shannon. It has a tidal range of approximately 5 m and is only 2 km wide at its narrowest point (Figure 5.1). It is an important habitat for Atlantic salmon (*Salmo salar*) (Inland Fisheries Ireland, 2015); the annual salmon migration provides a valuable food source for foraging dolphins, which are often seen chasing and tossing these fish (pers. obs.). The estuary is also an important industrial shipping lane, and a hub of fishing activity. It supports a local ecotourism industry, with two dolphin-watching companies operating during the months of April to October. The large amount of vessel traffic, combined with pollution risks from industrial and agricultural runoff, likely pose threats to the bottlenose dolphins resident in the estuary, as they are known to do for other cetacean populations (Jepson et al., 2016;

Nowacek, Wells, & Solow, 2001; Read, Drinker, & Northridge, 2006; Richardson & Würsig, 1997). Since the designation of the Shannon SAC, and in compliance with the Annex II reporting period, condition monitoring has been delivered via standardised boat-based surveys using mark-recapture photo-identification techniques to estimate dolphin abundance.

The dedicated monitoring transects cover an area of 150 km² in the lower Shannon Estuary. The ecotourism vessel selected for this study operates in an area approximately 67% the size of that covered by the dedicated surveys, closer to the mouth of the estuary (Figure 5.1).

5.2.2. Standardised surveys

Photo-identification surveys following a standardised 80 km route took place from June to October in 2015, in Beaufort sea state ≤ 3 , using a 6.5 m Rigid hull Inflatable Boat travelling at approximately 20 km h⁻¹. Trained observers continuously scanned the area on either side of the vessel until dolphins were encountered. Location, group size, and the presence of calves and neonates were noted. Photographs of dorsal fins were taken using an auto-focus DSLR camera (Canon EOS 1D mark II) with a 70–200 mm telephoto zoom lens. The transect route was resumed once all members of the group had been photographed (ideally from both sides) or when the group was lost. In order to minimise disturbance, if the dolphins showed evasive behaviour, the encounter was interrupted for five minutes and then resumed again. If the dolphins continued to avoid (or try to avoid) the boat, the encounter was terminated.

5.2.3. Platform of opportunity surveys

The POP used in this study was a 15 m commercial dolphin-watching boat conducting eco-tours at the mouth of the estuary, from April to October. Dolphin-watching tours are focused within a known core habitat area for this dolphin population (Ingram & Rogan, 2002).

Between June and August 2016, one to three eco-tours (hereafter referred to as trips) were conducted per day, depending on demand and weather conditions, each lasting 1.5–4 h. I was stationed on the POP on every trip, assisting with dolphin sighting during searches

and tracking during encounters, as well as recording data and photographing the animals. The route for each trip was roughly pre-determined by the skipper based on prevailing weather conditions. Trip effort was highly area-biased in order to maximise sighting success, that is, consecutive trips often targeted areas where there had already been a successful dolphin encounter on the previous trip or previous day.

When dolphins were sighted, they were approached slowly, staying to one side of the group so as not to disrupt the animals' activities. In accordance with dolphin-watching guidelines (Maritime Safety Directorate, 2005), each encounter was limited to a maximum of 30 min; if the dolphins appeared to actively avoid the boat, the encounter was abandoned. The sighting location, group size, number of neonates, calves, and juveniles, was recorded, as was the group's behaviour before and after being approached. Photographs of the dorsal fins of as many individuals as possible were taken using the same DSLR camera used on the standardised surveys.

5.2.4. Photo-identification process

The same photo-identification process was followed for both survey types. Individual animals were identified based on unique nicks and rakes on their dorsal fins and flanks. Photograph quality was graded (independently of the level of marking of each dolphin) from 1 to 4, with only the best quality photos (grades 1 and 2) included in subsequent analyses. Marking distinctiveness was ranked from 1 to 3, with 1 being assigned to animals with the most severely marked (and therefore most recognisable) dorsal fins, and 3 being assigned to animals whose dorsal fins were not permanently marked, but still identifiable within the limited sampling period. The best quality photograph of each side (where possible) of all photographed animals was selected and matched to an existing catalogue of individuals. If a match could not be made, the animal was added to the catalogue with a new, unique identification code.

5.2.5. Mark-recapture data analysis

As mark-recapture methods rely on the assumption that all animals are equally identifiable (Otis et al., 1978), only the subset of well-marked individuals (n_{marked}) with marking severity of 1 or 2 were included in the abundance models. This reduces the likelihood of

including false matches in the estimation process. The resulting estimates (\hat{N}) therefore represent the abundance of well-marked animals sampled during surveys. To obtain absolute estimates, the estimates of the marked population were inflated according to the proportion of marked individuals in the entire population, as follows. For n individuals identified within a sampling period, the proportion of well-marked animals is

$\theta = n_{\text{marked}}/n$. Therefore, the total abundance estimate for the entire population is

$N = \hat{N}/\theta$. Per Rogan et al. (2015), the variance of each total estimate ($\text{var}N$) was calculated using the delta method, that is:

$$\text{var}N = N^2 \frac{\text{var}\hat{N}}{\hat{N}^2} + \frac{1 - \theta}{n \theta}$$

Sighting history matrices (capture histories) were created for each subset of marked animals with the R package FSA (Ogle, 2017). Based on these capture histories, Chao's M_{th} models for closed populations were implemented in the program MARK, run via the R package RMark (Laake, 2013). All R analyses were run using version 3.5.0 (R Core Team, 2018). M_{th} models were selected because they account for heterogeneity in capture probabilities both over time and between individuals (Chao, 2001). This approach was applied to the 2015 dataset and to a number of subsets of the 2016 data, as described below.

5.2.6. Abundance estimate from dedicated surveys

Abundance estimates were calculated for 2015 using two methods. The first method was based on sightings of animals that had been identified from both sides. In the second method, separate estimates were calculated for animals identifiable only from the left or only from the right side (as not every animal in each encounter was photographed from both sides), after which the estimates were combined using inverse variance weighted averaging to obtain the final estimate. The model with the lowest coefficient of variation (CV) around the estimate was deemed most precise.

5.2.7. Abundance estimate from platform of opportunity surveys

Using the full dataset from 2016, two sighting history matrices were created, the first using each trip and the second using each day as a capture occasion. In the second approach, data from all trips within each day were pooled, meaning that an animal was only recorded once per day, even if it was sighted on multiple occasions during that day. This pooling was done to minimise possible spatial correlation of the data resulting from consecutive trips to the same area.

5.2.8. Calculating minimum effort required to derive reliable estimates

In order to calculate the minimum POP survey effort required to derive a robust abundance estimate, defined here as comparable to the full 2016 dataset estimate in both precision and accuracy, an iterative procedure was used to derive estimates with an increasing number of field days. For each of an increasing number of days (from 3 to 43), 100 randomly sampled days were selected from the full dataset and abundance estimates generated for each of the subsets. These were then compared to the point estimate generated from the full dataset (44 days); the minimum effort threshold was reached once all the abundance estimates consistently fell within the confidence intervals of the full estimate.

5.2.9. Minimising the spatial bias of the platform of opportunity

While pooling all trips within a day reduces the spatial bias of consecutive trips, it does not account for the autocorrelation between consecutive days, nor for the heterogeneity in the amount of effort between days. This creates a potential bias because each sampling occasion may not capture a representative sample of the population, which has not been given adequate time to mix, and because sampling was not conducted at random. An approach that reduces both of those potential issues is to consider each week as a capture unit, i.e., pooling data from all trips undertaken during a week. Using this approach, an abundance estimate was generated from the full dataset, which spanned 13 weeks. Moreover, as with the daily pooling, for each number of weeks from 2 to 12, the full dataset was randomly sampled 100 times. Each of the 1100 subsets generated was used to calculate an abundance estimate. These estimates were then compared to the one

calculated from the full 2016 dataset and, as before, the minimum effort threshold was considered to have been reached once all the estimates fell within the confidence intervals of the estimate calculated using all surveys.

5.2.10. Assessing the effect of sampling bias on abundance estimates

The area visited by the tour boat was smaller than the area covered by the dedicated surveys (Figure 5.1) and thus sampling of animals was restricted to a portion of the SAC. Therefore, any differences in individual habitat use may introduce sampling bias in the data collected from the tour boat, as some animals' ranges may be partially or entirely excluded from the survey effort. This would subsequently lead to heterogeneity in the individual sighting probabilities, potentially deflating the resulting abundance estimates. To investigate this potential source of sampling bias, maps of the ranging patterns of known individuals in this population were generated using data collected from previous dedicated surveys. Using the R package GISTools (Brundson & Chen, 2014), kernel density estimates based on the locations of animals sighted five or more times over the entire course (1997–2015) of standardised surveys were calculated and mapped over the full extent of the study area. Kernel densities were also mapped from the GPS tracks of the POP. For each animal i , the combined probability of being sighted by the dolphin-watching vessel in a given location ($P_{enc(i)}$) is equal to the probability of the animal being in that location ($P_{loc(i)}$, derived from all standardised survey years) multiplied by the probability of the POP being in that location (P_{POP} , derived from the tour boat's GPS tracks in 2016) (Figure 5.3). Dividing the combined probability of each animal being encountered by the POP anywhere in the estuary, $\sum P_{enc(i)}$, by the total probability of it being located anywhere in the estuary, $\sum P_{loc(i)}$, provides a proportionate estimate of the probability of finding an individual from the POP given the animal's range.

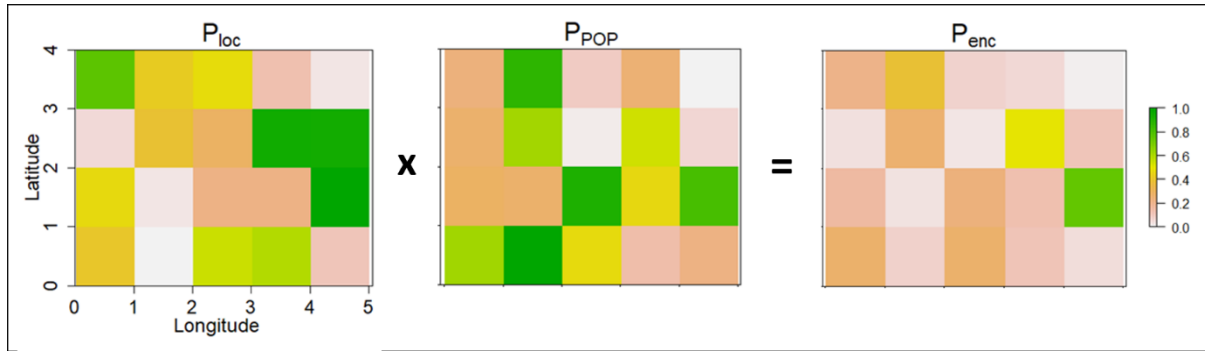


Figure 5.3. Illustration of the effect of spatially biased POP surveys on the probability of sighting an individual dolphin in a theoretical survey area. The first kernel density map shows the probability of a specific dolphin being in each of the grid squares. The second map shows the probability of the POP being in each of the grid squares. Multiplying the values of the two grids results in the third grid, showing the probability of the POP encountering that animal in each grid square. The sum of the final (P_{enc}) values is compared to the sum of the initial (P_{loc}) values, giving a standardised metric of the total probability of sighting the dolphin during a POP survey.

5.3. RESULTS

5.3.1. Standardised surveys

Between June and October 2015, 11 full dedicated transect surveys were completed, as well as one incomplete. These surveys resulted in 55 dolphin encounters, of 100 identifiable individuals. Median group size was six animals. Neonates were present in three encounters, and calves in 19. The rate of recruitment of new individuals to the dataset approached an asymptote over time (Figure 5.4), indicating that the population was closed during the sampling period.

5.3.2. Platform of opportunity surveys

Between June and August 2016, 78 dolphin-watching trips took place in good sighting conditions. The trips lasted an average of 2.6 h; total time on the water was 353.9 h, on 44 days. These trips resulted in 138 bottlenose dolphin encounters with a median group size of eight animals. Neonates were present in 18 encounters, calves in 71, and juveniles in 58.

The recruitment rate of new individuals to this dataset reached an asymptote after approximately 320 identifications, indicating that the population can still be considered closed for the purposes of selecting an appropriate abundance model (Figure 5.4).

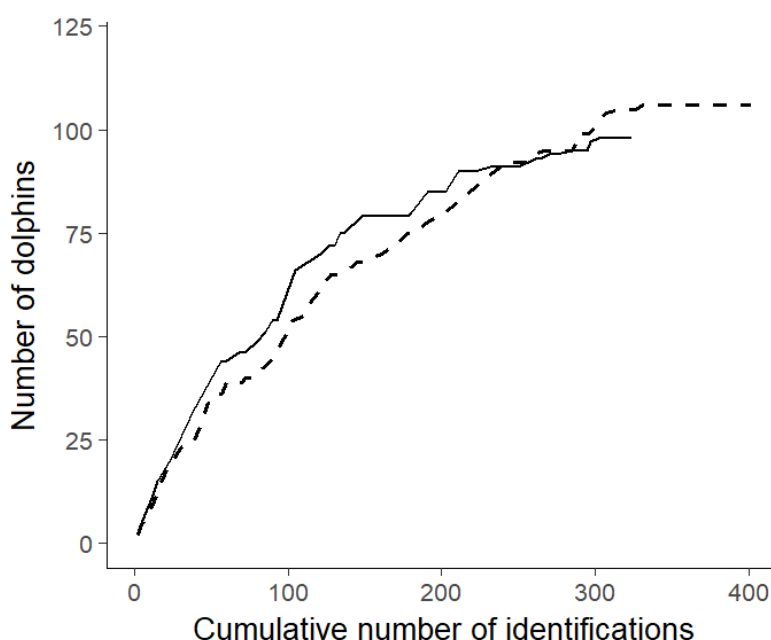


Figure 5.4. Discovery curves showing the rate at which new individual dolphins were identified during surveys in 2015 (solid line, dedicated surveys) and 2016 (dashed line, POP surveys).

5.3.3. Abundance estimates

The outputs from the abundance models are shown in Tables 5.1 and 5.2. In 2015, the weighted average model was more precise based on the CV than the one using animals known from both sides; the abundance estimate for the standardised surveys is 114 ± 13.5 (SE) dolphins. In 2016, there were too few animals identified from only one side to apply the same model averaging method as for 2015; therefore, only sightings of animals known from both sides were included in the analysis. A lower CV value was obtained by using trips rather than days as capture units; the abundance estimate for the POP surveys is 107 ± 8 (SE).

Table 5.1. Number of sampling occasions (capture units) and animals identified which generated abundance estimates of the bottlenose dolphins in the Shannon Estuary for the two survey years, 2015 and 2016. n = number of dolphins identified in initial population; n -marked=number of well-marked individuals; θ = proportion of marked individuals in n ; \hat{N} = abundance estimate for marked individuals.

Dataset	Capture units	n	n -marked	θ	\hat{N}
2015					
Both sides	12	61	43	0.71	90
Left side	12	50	35	0.70	53
Right side	12	53	39	0.74	85
2016					
Trips as units	78	106	74	0.69	75
Days as units	44	106	74	0.69	76
Weeks as units	13	103	73	0.71	76

Table 5.2. Abundance estimates of the bottlenose dolphins in the Shannon Estuary for the two survey years, 2015 and 2016. N= total abundance of dolphins; SE= standard error of N; CV= coefficient of variation of N; 95% CI= 95% confidence intervals of N.

Dataset	N	SE	CV	95% CI
2015				
Both sides	127	16.90	0.140	97–166
Averaged left & right	114	13.50	0.120	90–143
2016				
Trips as units	107	8.00	0.074	92–124
Days as units	108	8.26	0.076	93–125
Weeks as units	107	8.23	0.076	93–125

5.3.4. *Effect of sampling effort on estimate accuracy and precision*

The abundance estimates derived from increasingly larger subsets of the 2016 dataset are shown in Figure 5.5. As the number of days included in each subset increased, the estimates approached that generated from the full dataset. When including >35 days in the subset, all the abundance estimates generated fall within the confidence intervals of the full estimate, indicating that that is the minimum survey effort required to calculate an accurate abundance estimate. Moreover, the precision of the accurate abundance estimates, i.e., the ones derived from 35 or more field days, is progressively higher (as indicated by their low CV values in Figure 5.5).

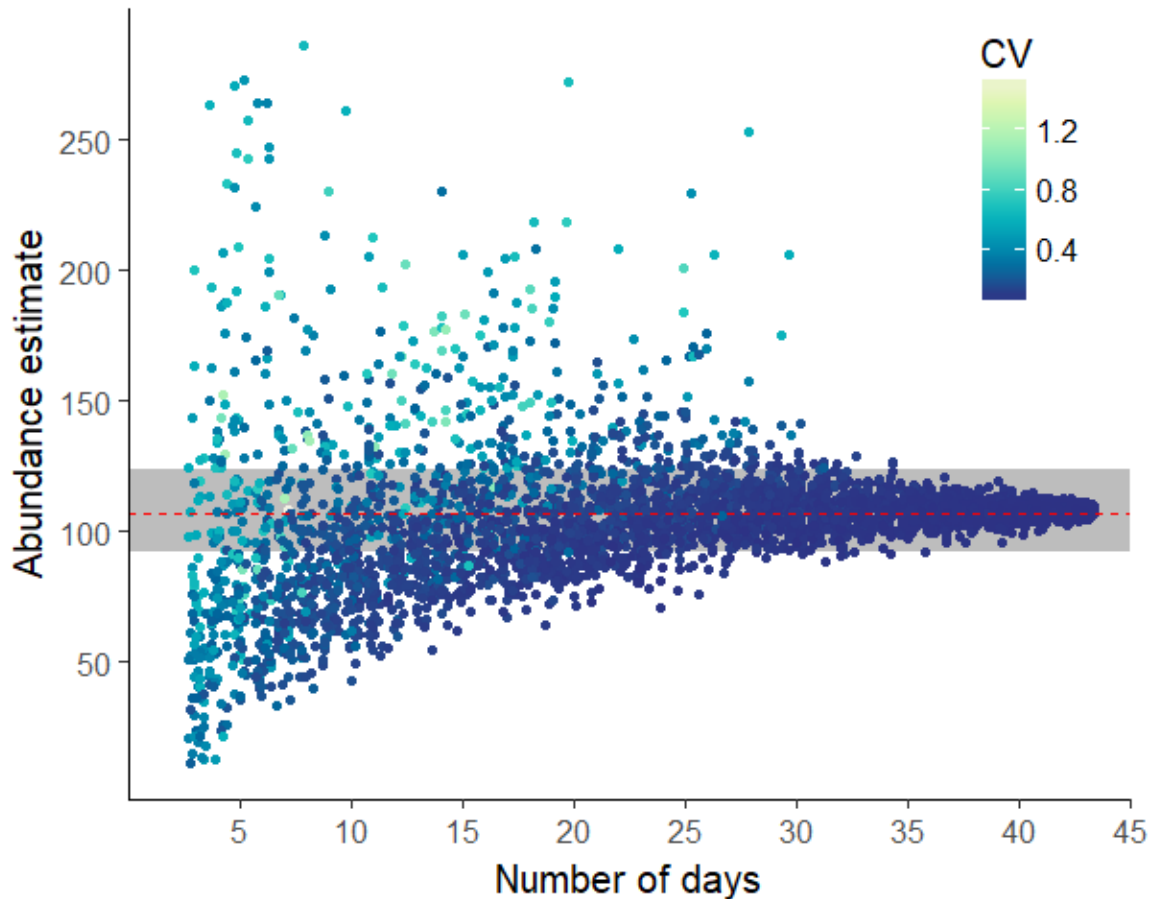


Figure 5.5. Abundance estimates (N) generated by randomly sampling an increasing number of days of mark-recapture data from the 2016 survey period. Each number of days was sampled 100 times from the full dataset. Colour gradient shows the coefficient of variation (CV) for each estimate; dashed line denotes the point estimate generated from the full dataset (45 days, $N=107$); shaded rectangle shows the 95% confidence interval of that estimate (92–124). Estimates that fall within the confidence interval are considered accurate.

5.3.5. Accounting for spatial bias of platform of opportunity surveys

Pooling the sightings data into weekly capture units to reduce the spatial bias caused by the possible autocorrelation of trips undertaken on consecutive days produced an abundance estimate of 107 ± 8.23 (SE); this is almost identical to that generated using trips as capture units (107 ± 8.00 (SE); Table 5.1). Using the same iterative process described above, increasing the number of field weeks included in the calculations leads to an increase in both accuracy and precision of the resulting abundance estimates; all the abundance estimates fall within the confidence intervals of the estimate generated from the full 13 field weeks (95% CI: 93–125) once ≥ 11 weeks are included in the dataset, while the CV values of the accurate estimates get progressively lower as the sample size is increased (Figure 5.6).

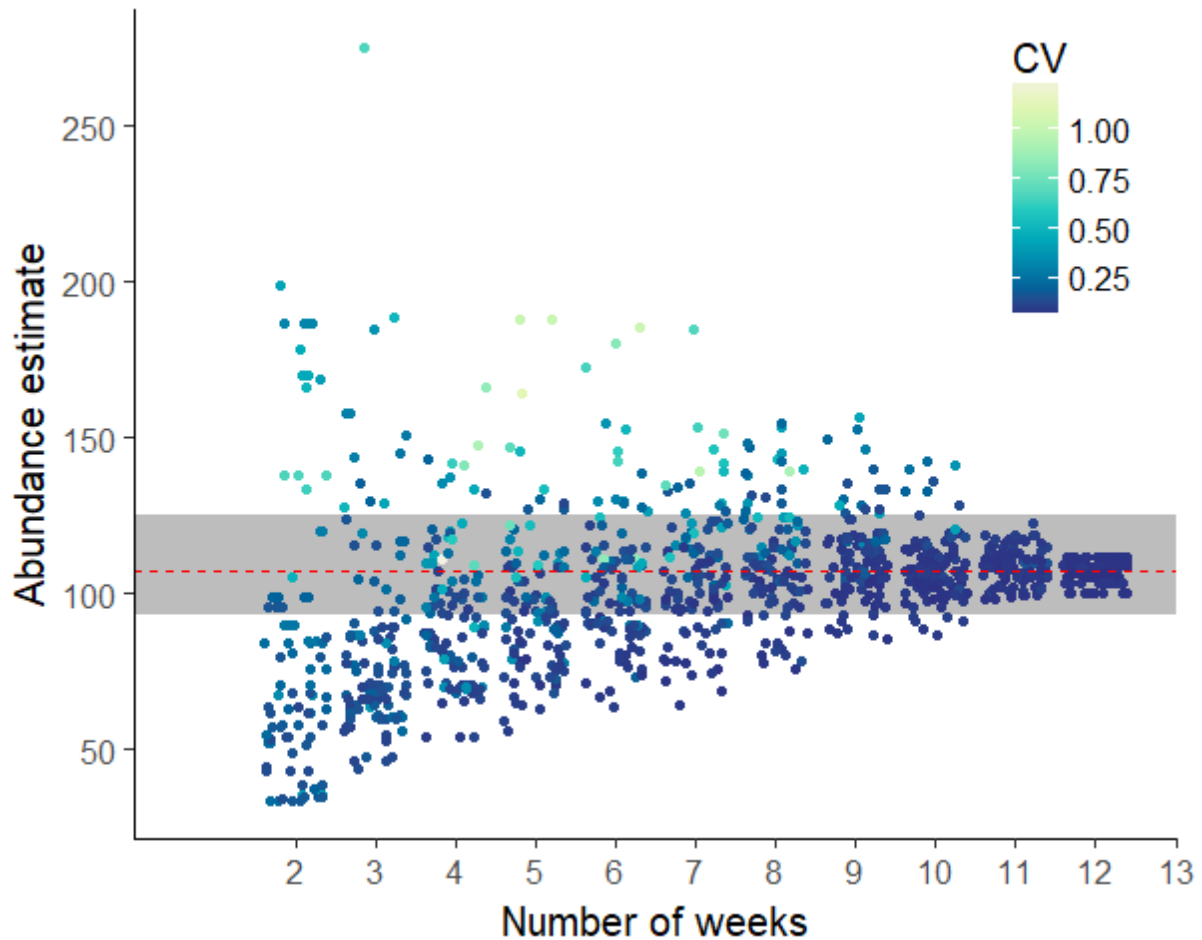


Figure 5.6. Abundance estimates (N) generated by randomly sampling an increasing number of weeks of mark-recapture data from the 2016 survey period. Each number of weeks was sampled 100 times from the full dataset. Colour gradient shows the coefficient of variation (CV) for each estimate; dashed line denotes the point estimate generated from the full dataset (13 weeks, $N=107$); shaded rectangle shows the 95% confidence interval of that estimate (93–125). Estimates that fall within the confidence interval are considered accurate.

While the discovery curve in Figure 5.7 indicates a fairly steady rate of recruitment of new individuals into the 2016 dataset before reaching an asymptote, the amount of survey effort undertaken by the POP each week varies (note the irregular spacing between weeks on the second x-axis). There is a marked increase in every effort metric (number of trips, number of hours on the water, number of dolphin encounters) towards the middle and end of the summer, with a subsequent drop-off during the last week. Taking 11 weeks to be the minimum threshold of effort required to generate an accurate abundance estimate, as calculated previously, this equates to approximately 68 trips, 69 dolphin encounters, 171 hours on the water, or 269 cumulative identifications, to reach the same result.

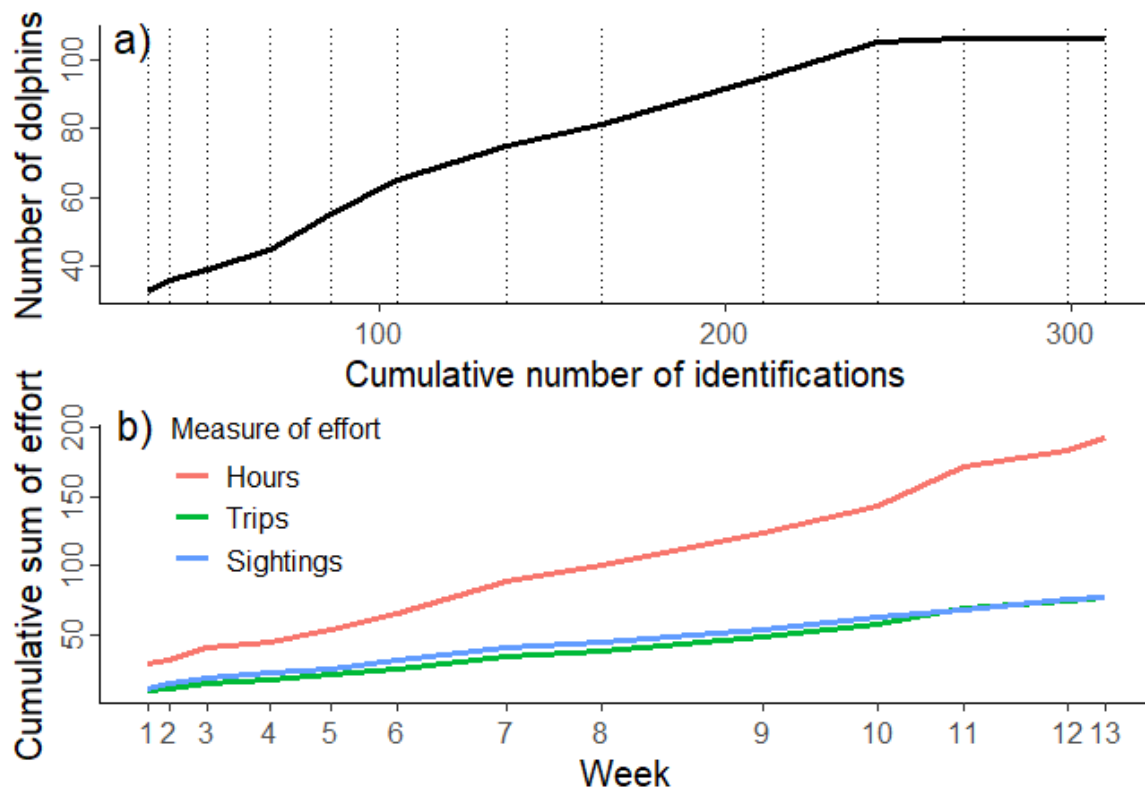


Figure 5.7. a) Discovery curve showing the rate at which new individual dolphins were identified over the course of the 2016 survey period, using weeks as capture units. Dotted lines indicate the end of each week of the survey period. b) Cumulative amount of effort required from week to week to produce the discovery curve. Note the uneven spacing between weeks on the lower x-axis; wider spaces correspond to a larger increase in effort than narrower ones.

5.3.6. Sighting probability of dolphins from the platform of opportunity

Given the entire range of each of the most frequently sighted individual dolphins within the estuary, the mean probability of each animal being encountered by the tour boat over the course of the summer is 0.40 ± 0.02 (SE). There is considerable inter-individual variation in encounter probabilities (Figure 5.8). Of the 80 dolphins used in this analysis, the average encounter probability from the POP was $\geq 50\%$ for 21 individuals and $\leq 25\%$ for 13 individuals. Only one animal (#462) shows a $\leq 5\%$ probability of being found within the POP's coverage, while another one (#103) has a 99% chance of being encountered there. The probability of these two dolphins being sighted from the tour boat throughout their known range is illustrated in Figure 5.9. The probability of an animal's being encountered by the POP was not related to the number of times it had been sighted over the course of all the standardised surveys.

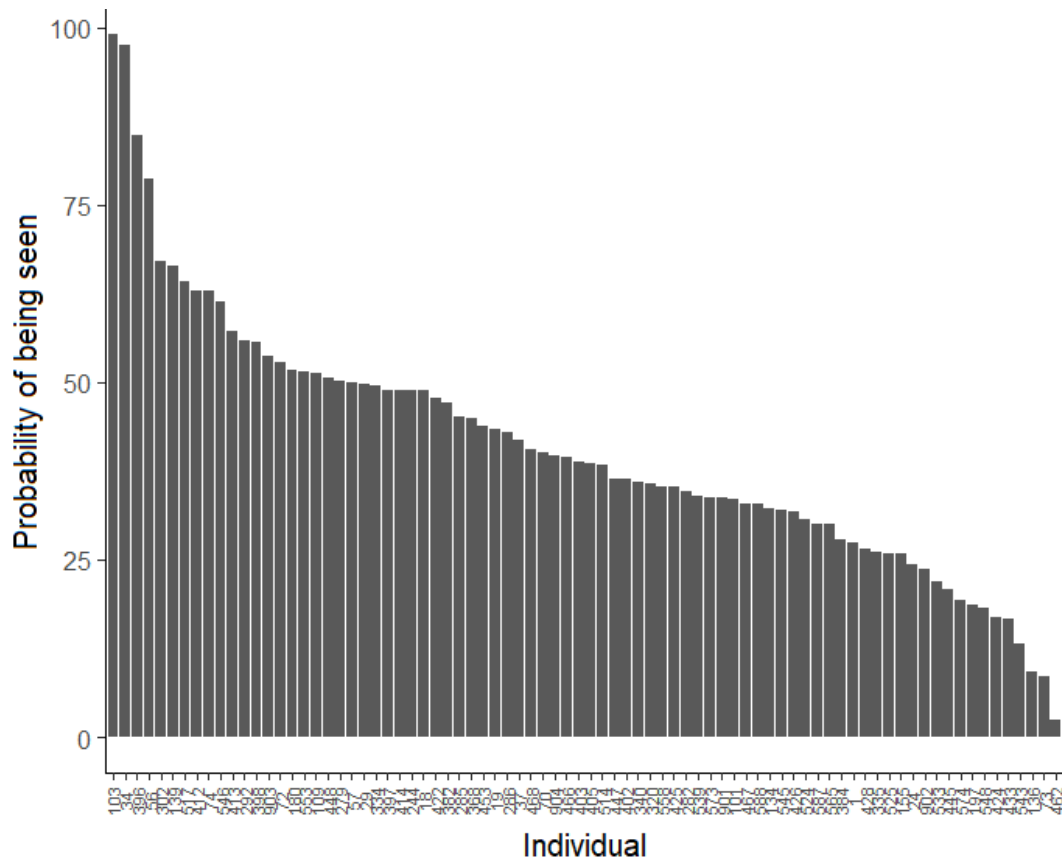


Figure 5.8. Encounter probability (%) from the POP for each of the 80 individuals sighted on at least five occasions in the Shannon Estuary survey area throughout standardised survey years (1997–2015).

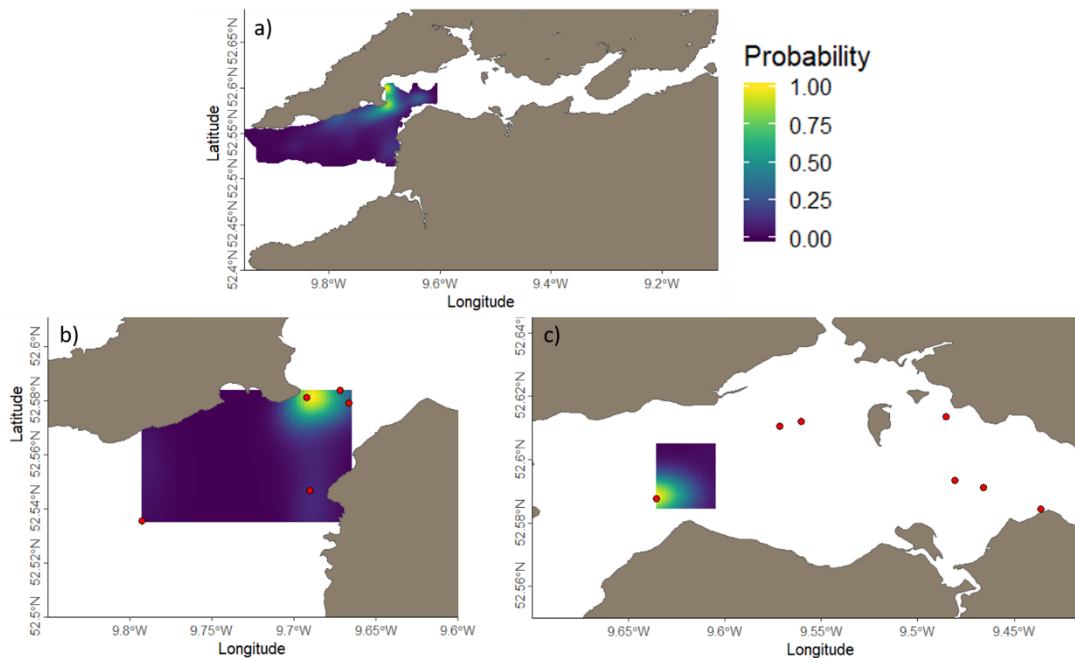


Figure 5.9. Probability of the POP encountering two frequently recorded dolphins within the Shannon Estuary, based on their sighting locations (points) throughout standardised surveys (1997–2015) and the movement of the tour boat (2016). a) Probability of the POP being anywhere in the estuary. b) Individual #103, which had the highest total probability of being encountered. c) Individual #462, which had the lowest total probability of being encountered.

5.4. DISCUSSION

This study demonstrates the utility of a POP to collect data suitable for estimating the abundance of a bottlenose dolphin population using photo-identification mark-recapture analysis. The use of POPs to determine cetacean abundance has been applied previously (Consiglieri et al., 1982; Moore et al., 2000); however, with a few exceptions where methods were similar to line transect surveys (Norrman, Dussan-Duque, & Evans, 2015; Williams et al., 2006), it has not been combined with mark-recapture methods. The results from the POP used in this study were similar to those derived from dedicated photo-identification surveys in previous years, indicating its suitability as a complementary method to the standardised methods that are already in place.

The abundance estimate derived from the standardised surveys in 2015 served as a baseline to which the POP survey results were compared. This estimate is consistent with estimates reported during previous years (e.g., Berrow et al., 2010), and with a precision level ($CV=0.12$) recommended by Englund et al. (2007) for this population. The abundance estimate generated using the data collected from the POP in 2016 was also comparable to the 2015 estimate, and more precise ($CV=0.08$); therefore, it can be considered a robust estimate if there has been no dramatic change in population size between the two years.

Spatial bias in the operation of the POP introduces heterogeneity into the capture probabilities of encountered individuals, due to differences in their ranging behaviour within the SAC. Pooling the data into larger capture units, such as days or weeks, helps to reduce some of this heterogeneity by allowing the population more time to mix, as well as the bias caused by revisiting the same locations between consecutive trips (within a day) and consecutive days (within a week). In each case, both the accuracy and precision of the resulting abundance estimates were retained and were nearly identical to the estimate generated from the full dataset when using each trip as a single capture unit.

The detection probability analysis showed considerable capture heterogeneity among individuals in the smaller area covered by the POP. This variation of individual detection probabilities resulting from biased sampling effort, combined with variation in animal ranges, illustrates why more survey effort is required to produce a robust abundance estimate from a POP compared to that required during dedicated surveys. Individual dolphins clearly frequent different parts of the estuary, some remaining primarily upriver for the duration of the sampling period and others ranging in a larger area (Ingram &

Rogan, 2002). As the tour boat covers a smaller area restricted to the lower estuary, the likelihood of an animal that spends most of its time upriver being encountered in the lower estuary is slight, unless effort is increased considerably. As the number of sampling occasions increases, the negative bias introduced by heterogeneity in capture probability is reduced.

In this study, the minimum effort required to generate an estimate comparable to the one generated by using the entire dataset was calculated in terms of several effort metrics. Repeated sampling of days indicates that a minimum of 35 field days are required to gather sufficient data, while random sampling of weeks indicates that 11 field weeks are necessary to derive an estimate with a similar precision to that derived from a dedicated survey. Note that there is no real disparity in these numbers, since the average number of days per week during which trips took place in 2016 was 3.2 ± 0.44 (SE). From a monitoring perspective, if the data are to be processed in daily capture units, it is recommended that the days in which observers are placed on the tour boat are spaced out, e.g., every other day, rather than on consecutive days. This would require the survey period to extend earlier and/or later into the dolphin-watching season, which may be logistically more difficult. If the data are pooled into weekly capture units, the effect of spatial bias of the eco-tours is minimised, so conducting observations on consecutive days would not pose an issue.

The effort required to obtain an accurate estimate of population size using photo-identification from a POP, whether measured in trips, days, hours on the water, encounters, or even cumulative dolphin identifications, is considerably higher than that required during dedicated monitoring surveys. Because of the higher number of encounters, there is a proportionately higher number of photographs to process when using a POP, so the photo-identification process also takes longer and requires more labour than for a standardised survey. However, there are a number of benefits of using POPs. Firstly, the cost of placing an observer on a POP for a day is small compared to the daily cost of a standardised survey, which involves paying for boat fuel and maintenance, as well as towing vehicle fuel or boat berth rental (depending on whether the research vessel needs to be towed to the study area or not). Similarly, the logistical difficulties of deploying a research vessel (which cannot be done by one person), and working often within constrained weather windows, are bypassed when it comes to placing one trained photographer aboard a tour boat for an extended period of time. As a result, it should be feasible to conduct POP surveys more frequently, filling in the gaps between dedicated

survey years. Englund et al. (2007) showed that frequent monitoring of this population is crucial and that the current reporting scheme would not be able to detect a 5% per year decrease before the number of dolphins in this population was reduced by 50%. Annual monitoring with a $CV \leq 0.12$, on the other hand, would detect a 5% decline before the population was reduced by 38%. Furthermore, as the dolphin-watching boat operates every year, regardless of whether a standardised survey is taking place, using it as an interim platform rather than increasing the frequency of standardised surveys means that the observers are not adding to potentially harmful boat noise and traffic by using a dedicated research vessel. As pointed out previously, the tour boats in this area follow a strict protocol to minimise disturbance, so using them as a research platform does not in itself add to the existing threats to the dolphin population. The increased frequency of monitoring the population, however, will provide more thorough insight than the sporadic dedicated surveys currently in place, thus better informing conservation and management decisions.

A further noteworthy benefit to increasing the frequency of mark-recapture surveys is the maintenance of up to date photo-identification catalogues. Whereas changes in the natural markings of individuals within the short duration of a sampling period are usually not dramatic enough to lead to misidentification (Williams et al., 1993), over the course of several years these markings can accumulate to the point where a dolphin is no longer recognisable and is entered as a new individual into the reference catalogue. This leads to a loss of continuity in individual data and may result in bias in the estimation of population demographic parameters; i.e., the false assumption that an animal has been lost—died or emigrated—from the population and that another one has entered the area. Yearly surveys would serve to keep catalogues up to date, as the accumulation of changes in the dorsal fin markings is easier to track. Long-term monitoring of individuals is useful in studies of movement patterns and inter-individual behavioural differences (Würsig & Jefferson, 1990) and could also provide crucial demographic data that cannot reliably be inferred from the standardised surveys, due to their infrequent nature. Information such as birth rates, calving intervals, and survival rates, would give greater insight into the resilience of the population in the face of existing threats and potential disturbances. Moreover, as a result of spending more time on the water during a POP survey year, the re-sighting rate of individuals will be higher than during standardised survey years. Since the precision of association indices increases with the number of observations of each individual (Whitehead, 2008), this would allow more detailed inferences about the population's social

structure within a season, as well as how stable this is from year to year than gleaned from the dedicated surveys.

The utility of photo-identification techniques in estimating population size from a POP depends on the type of the platform, as well as the species and population in question. In this study, the method proved robust because the dolphin-watching boat covered a sufficiently large part of the known range of the dolphin population, and the identified animals had (to varying degrees) overlapping ranges. The same method would not be suitable in the case of extremely spatially restricted vessels, such as ferries—unless the fraction of the habitat surveyed is critical for the population, so that a sufficient number of individuals moves through it frequently enough to be encountered. In addition, if there is greater disparity between individual home ranges, sampling a smaller area will likely pose a more significant problem than in the present study. Consequently, the effect of such a spatial restriction should be measured before implementing a POP-derived abundance estimate.

Another prerequisite for population monitoring using this approach is high survey frequency. The mark-recapture model used here relies on a sequence of observations (applied to a closed population), ergo, attempting it from a single bout of effort or rarely repeated transects (e.g., a cruise ship that only follows the same route once a year) would not be appropriate. Ecotourism vessels are better suited to this type of study, provided that photo-identification is applicable to the cetacean species under observation. Examples where ecotourism vessels cover part of the range of photo-identifiable cetacean populations include Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong (Jefferson, Hung, & Würsig, 2009), Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand (Palliser & Dodson, 2017), killer whales (*Orcinus orca*) in the Pacific Northwest and several Mysticete and Odontocete species in the Persian Gulf (Nouri, Danehkar, & Sharifipour, 2008). There are also a number of other resident bottlenose dolphin populations in Europe and elsewhere, around which dolphin-watching industries have developed, such as in the Sado Estuary in Portugal, Cardigan Bay in Wales, and the Moray Firth in Scotland. When the observed population can be considered closed for the duration of a survey period, the methods outlined in the present study can be applied. In the case of an open population, the models used to estimate abundance should be selected accordingly.

Whale- and dolphin-watching vessels are POPs that have long contributed to cetacean research and conservation efforts (Hoyt 2001), driven in part by the exponential increase in marine tourism since the 1960s (Higham et al., 2016). It is important to note, however, that these vessels also pose risks to the animals being studied. Disturbance from tour boats can impact cetaceans, disrupting their normal behaviours, increasing ambient underwater noise, or even directly resulting in mortality in the case of collisions and the separation of young calves from their mothers (Parsons, 2012; Senigaglia et al., 2016). Even in such cases where negative effects aren't clearly discernible (Di Clemente et al., 2018) or the animals habituate to tour boats after prolonged exposure (Richter, Dawson, & Slooten, 2006), long-term sub-lethal effects cannot be discounted (Christiansen, Rasmussen, & Lusseau, 2013; Pirotta et al., 2015). Moreover, the presence and stringency of codes of conduct surrounding whale-watching activities varies considerably depending on the region (Garrod & Fennell, 2004). Therefore, it is advisable to consider the specific implications for the cetacean populations in question prior to taking advantage of such opportunities.

This study shows that a POP can be a useful supplementary monitoring tool for a bottlenose dolphin population. Given the cost of dedicated surveys, it is unlikely that their frequency will be increased to an annual basis. The current monitoring scheme in Ireland could be complemented by POP surveys in years when standardised surveys are not conducted. The incorporation of POP survey data would enhance our ability to detect declines in abundance or site use earlier than by infrequent conventional surveys alone, allowing appropriate conservation measures to be put into place sooner. In addition, annual surveys will allow more detailed demographic parameters to be estimated, providing insight into the structure of this genetically isolated population. This method could also be applied to several other species, some of which are critically endangered and require frequent monitoring. POPs can, in this way, be a considerable conservation asset, especially in regions where funding is lacking.

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Chapter 6. GENERAL DISCUSSION

The study of a species' distribution and habitat preferences is integral to its effective conservation (Whittaker et al., 2005). Yet when it comes to marine mammals, understanding their habitat preferences is often a challenging task. Due to the nature of both the animals themselves and their environment, direct visual observations can be difficult to obtain—as Mitchell & Webb (2009) point out in a discussion about counting whales, not only do these animals have access to an infinitely large (for all practical purposes) body of water to roam in, they also spend a considerable amount of time under said water, “which we, in our [research vessel], try to avoid doing.” That is to say, cetaceans can range over wide areas to take advantage of patchily distributed resources, and not knowing *a priori* why and how a species targets these patches (whether for food or shelter or as breeding grounds) makes it hard to design surveys of an appropriate size and frequency to detect patterns, not to mention the logistical issues related to rough seas, poor visibility, and trying to detect animals that only surface for brief periods of time.

Even once we overcome the challenges posed by an often harsh or inclement environment (e.g., by conducting visual surveys in good weather, using acoustic monitoring techniques when visual surveys are impossible or combining the two, scaling observations up from an individual to a population level through advanced mathematical modelling, etc.), we still cannot always detect patterns accurately. Habitat use even within a single population can vary depending on age (e.g., adult grey whales *Eschrichtius robustus* in British Columbia use different habitat types and feed on different prey species than calves; Darling, Keogh, & Steeves, 1998), reproductive status (humpback whales *Megaptera novaenglia* in Brazil prefer shallower waters when accompanied by calves; Martins et al., 2001), sex (e.g., adult male and female sperm whales *Physeter macrocephalus* only use the same areas during breeding season; Whitehead & Weilgart, 2000), or social structure (e.g., each of three different pods of the Southern Resident killer whales *Orcinus orca*, use areas that overlap very little between the social groups; Hauser et al., 2007). The adaptive nature of certain cetacean species makes it even more difficult to understand their habitat use, because they may respond differently, in a habitat-specific manner, to the same environmental variables. For instance, the common bottlenose dolphin (*Tursiops truncatus*) is known to inhabit a range of different habitat types the world over, from the open ocean to small bays and estuaries (Wells & Scott, 2009). A single population's range can encompass a variety

of habitat types and prey distributions, and its individuals adapt their movement patterns and behaviours accordingly. For example, Hastie et al., (2004) found that bottlenose dolphins in the Moray Firth tend to forage more in deeper waters with steep seabed gradients than elsewhere, with this behaviour peaking in summer months, likely as a response to migrating fish. Their distribution in the area, therefore, also has a dynamic, seasonal component, in relation to changing environmental parameters. Dynamic oceanographic and hydrographic features have been found to explain the variability in cetacean distribution patterns as much as static ones (Yen, Sydeman, & Hyrenbach, 2004; Tynan et al., 2005; Worm, Sandow, Oschlies, Lotze, & Myers, 2005; Bailey & Thompson, 2010); thus, temporal variation in distribution is apparent, as well as spatial variation. Different features can play a role on different scales, as well; for instance, in the open ocean, changes in temperature or productivity can influence cetacean distribution over a large spatial or temporal scale (e.g., seasonal changes in sea surface temperature are related to offshore movements of short-beaked common dolphins *Delphinus delphis* in New Zealand; Neumann, 2001), while fine-scale hydrographic and topographic features can explain occupancy patterns and behaviour at a much finer scale (e.g., daily changes in tidal height can affect harbour porpoise foraging patterns in Wales; de Boer et al., 2014).

Ireland's EEZ is more than ten times the size of its landmass (*Harnessing our ocean wealth*, 2012). Its position close to the European continental landmass on the east and the exposed Atlantic waters to the west create high oceanographic variability across the region (Casal et al., 2015). Sea surface temperatures are affected by the influx of warm Atlantic water onto the Irish continental shelf, while coastal waters are even more strongly influenced by freshwater runoff and are thus generally colder in winter and warmer in summer than the offshore waters (O'Boyle & Silke, 2010). Currents and upwellings around the coastline are formed by the differences in salinity and temperature, but are primarily wind-driven in waters west of the island (DECLG, 2013). These oceanographic features make the Irish marine zone highly productive and diverse, supporting important spawning grounds for pelagic fish stocks, such as mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), and blue whiting (*Micromesistius poutassou*) off the west coast, hake (*Merluccius merluccius*) and megrim (*Lepidorhombus whiffiagonis*) along the continental slope, and herring (*Clupea harengus*), cod (*Gadus morhua*), plaice (*Pleuronectes platessa*), and sole (*Solea solea*) in the Celtic and Irish Seas; important nursery grounds for young fish are found both coastally and across the continental shelf

area (Gerritsen & Lordan, 2014). This diversity of environments and potential prey species is likely a key factor influencing the distribution of bottlenose dolphins in the region. However, this same diversity—and our imprecise knowledge of its exact parameters—also makes it challenging to determine how bottlenose dolphins use their environment, given their flexible habitat use.

This thesis comprises a comprehensive investigation of the habitat preferences of common bottlenose dolphins within the Irish EEZ, as well as the potential of conducting abundance monitoring from a platform of opportunity. More specifically, I studied the habitat use patterns of three distinct dolphin populations, the ranges of which vary in size. The results highlight the fact that the habitat use and site occupancy patterns of these populations are not all related in the same way to the same environmental variables. Though the modelling techniques applied in each case were similar—adapted to the spatial and temporal resolution of the available data in each case—there was considerable variation in the significance and shape of relationships between dolphin occurrence and environmental variables.

6.1. Large scale

One of the populations studied was the “pelagic” one, which inhabits waters >4 km away from Ireland’s coastline (Oudejans et al. 2015); it is genetically distinct from a putative “coastal North” population that was proposed by Louis et al. (2014a), as well as socially isolated from coastal dolphin communities. Besides showing no evidence of site fidelity in this population, Oudejans et al. (2015) found significant differences in scarring patterns between the coastal and pelagic communities; namely, pelagic animals had higher overall degrees of scarring and distinctive injuries to the tip of the dorsal fin, which were rarely observed in coastal animals. The authors of that study suggest that the offshore population likely interacts more with commercial fisheries and is at higher risk of fishing gear injuries; this would be consistent with scarring patterns observed in false killer whales (*Pseudorca crassidens*) in Hawaii (Baird et al., 2015). Whether or not that is the case, these differences between populations do constitute evidence of diverging behaviours and interactions with their respective environments (whether with conspecifics, predators, or human activities deserves to be further investigated), which could be the result or possibly as the cause of their differences in distribution and ranging patterns. The absence of site fidelity and any long-term associations between individuals in the pelagic population are similar to

patterns found in other offshore dolphin communities and species, which display a more fluid social structure and are known to travel over longer distances (>100 km) (Silva et al., 2008; Scott & Chivers, 2009) than coastal populations.

Modelling of the habitat preferences of this pelagic population supports the hypothesis that the links between environmental variables and distribution are habitat- and season-specific (see Chapter 2). While, for instance, there were significant correlations between sea surface temperature and bottlenose dolphin presence, the shape and significance of these relationships changed between winter and summer and between shelf and abyssal waters. Habitat-specific responses to environmental changes have been documented in other taxa, e.g., fish communities in the Baltic Sea respond to climatic variables on a local rather than regional scale (Östman et al., 2017), basking sharks (*Cetorhinus maximus*) show opposite daily vertical migration patterns depending on whether they are feeding in shelf or deeper, well-stratified waters (Sims et al., 2005), and Risso's dolphins (*Grampus griseus*) show variable responses to the same dynamic model parameters depending on their location (Soldevilla, Wiggins, & Hildebrand, 2010).

It is not surprising, therefore, that the pelagic population shows variable responses to the same environmental parameters, given its wide distribution across such distinct habitat types (continental shelf, slope, and abyssal waters). They may have different dietary preferences and foraging specialisations depending on this broad habitat classification and their prey in each region is likely to be influenced in different ways by temperature, productivity, frontal systems, and habitat complexity (as reflected by seabed rugosity). Moreover, their ranging patterns may be affected by the occurrence of competitor or predator species in some habitat types. For example, sixgill sharks (*Hexanchus griseus*) are known to prey on bottlenose dolphins in some areas, but are predominantly found in deeper waters along the continental shelf edge and upper slopes (Heithaus, 2001); if their distribution is affected by dynamic variables, the bottlenose dolphins in those habitats might respond differently to the same environmental changes than the ones where these sharks do not occur. Whether or not these distinctions in habitat use are also indicative of finer population structure (e.g., non-overlapping social groups or subpopulations) or whether all bottlenose dolphin groups encountered in this survey belong to a single, homogeneous population that ranges throughout the Northeast Atlantic margin is worthy of detailed investigation.

To address this question would require several finer-scale surveys throughout the pelagic population's known range, to collect data on social structure (e.g., through photo-identification) and genetic diversity (through biopsy sampling). Photo-identification could also be used to investigate movement patterns if individuals are re-sighted at distant locations. A more effective way to model movement patterns, perhaps, would be to tag individuals and track their movements over a period of several hours or days to understand how quickly and how far they move on a daily basis. The logistical implications of such an undertaking would be considerable. For instance, there would be need of a large vessel to traverse the distances required safely and efficiently, whereas conducting photo-identification or biopsy sampling on the comparatively small and fast-moving bottlenose dolphins would require a lower and easier to manoeuvre platform (e.g., a RIB), as would any attempt to attach tags to these animals. Moreover, the surveys would have to be conducted repeatedly to maximise sample size and individual re-sighting probability. Another important aspect would be international collaboration, in order to ascertain the geographic extent of this population. Distinct coastal and pelagic ecotypes of bottlenose dolphins have been established in the Northwest Atlantic (Vollmer & Rosel, 2017), but the differentiation between offshore individuals on that side of the ocean and the ones on the eastern side is lower than between coastal and pelagic populations on either side (M. Louis, pers. comm. 2019), making it more challenging to delineate population structure. Neither has it been ascertained whether the dramatic difference in estimated bottlenose dolphin abundance between the first and second year of the ObSERVE surveys—especially in the second winter season—is due to an influx of animals from more northerly, southerly, or westerly waters, or a combination thereof. It would be beneficial to conduct concurrent large-scale surveys both across the Irish EEZ and beyond in order to determine whether there is a directional movement of animals on a seasonal or inter-annual basis.

6.2. Intermediate scale

The “coastal mobile” population ranges along the west coast of Ireland; as well as being separate from the pelagic population, it is also demographically and genetically distinct from the other coastal population, which resides in the Shannon Estuary. Its precise home range size is not known. Oudejans et al. (2015) found that these animals do not move beyond 4 km from shore. However, Robinson et al. (2012) documented individual animals from this population in UK waters, suggesting that, while they may not mix with the

offshore community, they are not all confined to this narrow band along the Irish coastline. Ingram, Englund, & Rogan (2001) identified a few key areas that seem to play an important role for the population, but continued monitoring efforts of the entire coastline are logistically challenging.

Passive acoustic investigation of dolphin site occupancy in two locations on the west coast showed a decided seasonal difference in each area, as well as site-specific response to increasing surface temperature in the wider vicinity. While tidal level affected dolphin presence in both sites and, likely, has to do with prey aggregation (as discussed in Chapter 3), the temporally finer-scale models (hourly and daily) did not fit the observed data at all well, in contrast to the monthly model. Different variables can influence species distribution at different scales; the finer-scale models included fine-scale habitat characteristics, which may not necessarily play such a critical role for a population with intermediate ranging patterns. That is, the influence of broader parameters such as chlorophyll concentration and surface temperature may better explain further movements between sites.

Noticeably, sea surface temperature was a significant predictor only in the northern of the two study sites, where dolphin presence directly increased with increasing temperatures. In colder months ($SST < 12^{\circ}\text{C}$), McSwyne's Bay generally had lower temperatures than Killary Fjord, the difference ranging from a fraction of a degree to almost 2°C (Figure 6.1, below). For temperate species at the northernmost extent of their range, small fluctuations in temperature may have a more noticeable effect on an animal than at lower latitudes. This could apply to the physiology of the dolphins themselves or that of their prey. Yeates & Houser (2008) suggest that water temperature alone is not enough of a limiting factor for bottlenose dolphins weighing $> 187\text{ kg}$, but that colder waters may restrict the northward range of smaller individuals (neonates, calves, and their accompanying females), especially when combined with factors such as prey distribution. Temperature affects the survival and growth rates of larval and juvenile fish stages (e.g., Buckley, Caldarone, & Lough, 2004), as well as water stratification and nutrient mixing, both of which can have knock-on effects on higher trophic levels. Subtle changes in temperature were found to be important predictors of blue whale (*Balaenoptera musculus*) and sea turtle (*Caretta caretta*, *Chelonia mydas*, *Lepidochelys olivacea*) foraging hotspots (Etnoyer et al., 2006). Moreover, northward shifts of distribution ranges following incremental temperature changes as global oceans warm have been documented and are

predicted for several marine species, from barnacles (*Austrominius modestus*, Gallagher et al., 2015) to fish (Morley et al., 2018) to entire benthic communities (Hiscock et al., 2004). Looking again at Figure 6.1, it appears that the extreme surface temperatures in McSwyne's Bay were always more pronounced than in Killary Fjord, that is, lower minimum temperatures and higher maximum temperatures overall. This difference in temperature variability no doubt affects the composition of prey communities in each location and could indicate that prey aggregations in the northern site are less predictable than in the southern one, and therefore the former area is visited less regularly by foraging dolphins. Detailed studies of the abundance and seasonal presence of fish species in each area would help to address this question. As a similar association with milder waters (especially in winter months) was also observed in the offshore population, it is clear that sea surface temperature is an important factor for bottlenose dolphins at both large and intermediate scales in Irish waters.

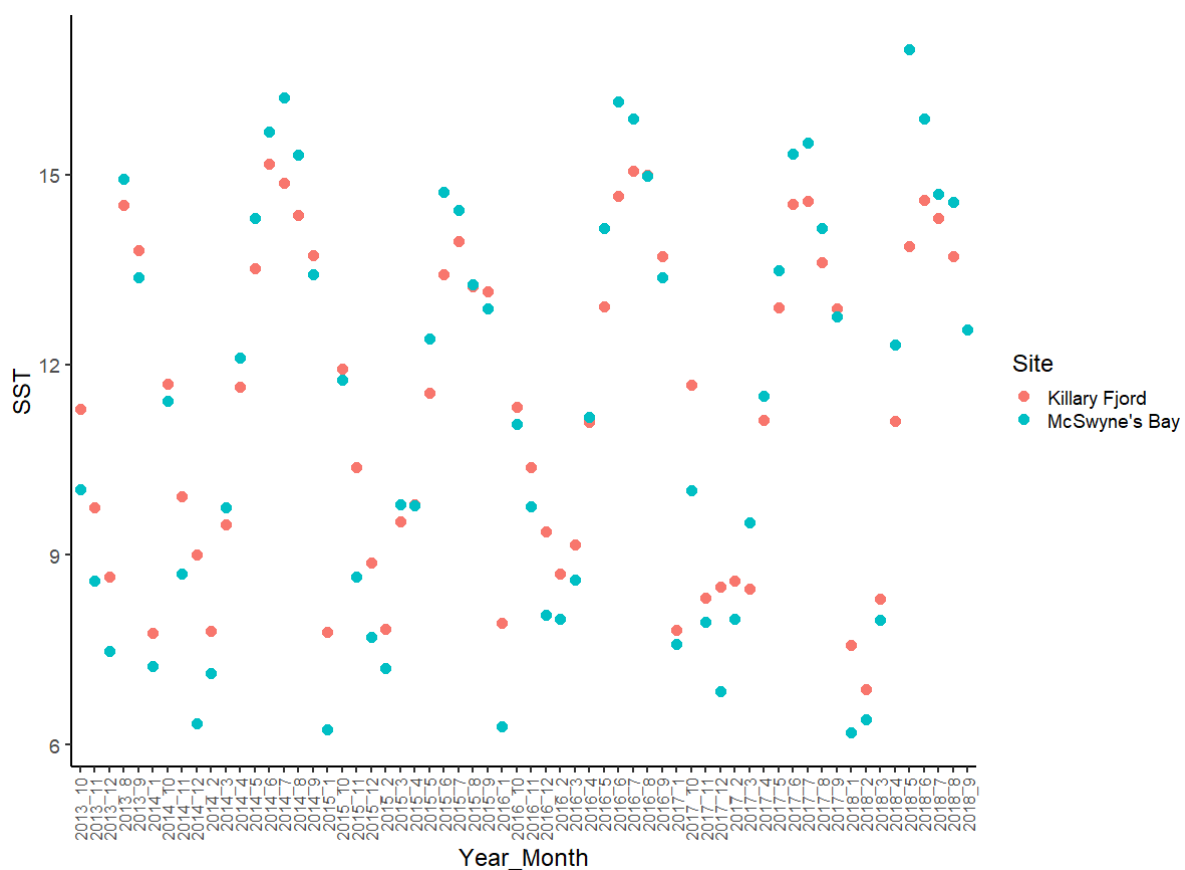


Figure 6.1. Average monthly sea surface temperature (SST) of two 8 km x 8 km areas encompassing the deployment sites of the C-PODs during five years of deployment (2013 to 2018).

6.3. *Fine scale*

The third population studied also happens to be the most well-studied of the ones presented here. These bottlenose dolphins are resident year-round in the Shannon Estuary and are genetically and socially distinct from the other two populations. This isolation could render them more vulnerable to extinction risks, as there seems to be little or no mixing with other populations and thus any population decline could be hard to recover from. As such, it is important that population trends are closely monitored. However, as was outlined in Chapter 4, abundance estimates alone may not provide a complete picture for adequate marine spatial planning. Knowing how these animals utilise different parts of their habitat and how they are affected by dynamic environmental characteristics is equally important, because it makes protecting key features or predicting risks easier in the face of anthropogenic pressures. It is not enough to determine the locations these animals prefer, without knowing why they are attracted to specific features, in an environment subject to direct and indirect human intervention (e.g., dredging, widening or narrowing deep-water channel, increasing vessel traffic, allocation of fishing licences and quotas).

The Shannon Estuary is a unique area on the Irish coast. Its location at the mouth of the longest river in Ireland, with all that implies about nutrient outflow, migrating fish stocks, and shelter from oceanic predators, coupled with the hydrographic features described in Chapter 4, make it a very favourable habitat for bottlenose dolphins. It is unclear when this population split from the other coastal one, but Nykänen et al. (2018) inferred that this occurred much more recently (less than a few thousand years ago) than the original founding event(s) of the Coastal North population by members of the pelagic population. In the present day, these animals' movement patterns are affected primarily by temporally and spatially fine-scale features, in contrast to the mobile coastal and pelagic populations. It is difficult to predict how this population might be affected by broader-scale changes in their environment. The abundance and distribution of their current prey species will likely change in the near future as a result of climate change (Graham & Harrod, 2009; ter Hofstede, Hiddink, & Rijnsdorp, 2010; Cheung et al., 2011). Whether or not the dolphins will adapt to any changes in prey availability as they have been known to do elsewhere (Ansmann et al., 2012) remains to be seen.

Before such changes take place, however, and with the aim of detecting them when and if they do occur, continued monitoring of the population's status is imperative. Given the current infrequent nature of standardised abundance surveys in the area, the potential of

a dolphin-watching boat as an interim alternative platform to get similar estimates was investigated. The results were encouraging (see Chapter 5) and are further validated by the results of the habitat models presented in Chapter 4. To elaborate, the platform of opportunity used operates primarily in the lower estuary, which the models identified as important for the dolphins at certain times. Having identified different “hotspots” of use depending on the phase of the tidal cycle, if the dolphin-watching boat were to be used as a monitoring platform, it would be easier to plan “survey” effort (i.e., placing an observer on board the boat) around times when the lower estuary is in peak use by the dolphins, maximising the likelihood of encountering sufficient individuals to get a robust estimate. Care must be taken, however, to ensure that these areas are used by a representative sample of the population and not merely the same few individuals repeatedly. A more detailed look at individual habitat use in the area would address this issue. Moreover, it would be interesting to compare habitat use patterns as identified from the platform of opportunity to those found in these models. McBride-Kebert et al. (2019) used sightings data from tour boats in Florida to identify hotspots of dolphin presence. The areas highlighted as important in that study differed from their findings based on standardised surveys, because of the spatially biased movement of the tour boats and the lack of associated tracklines. In the Shannon Estuary, however, the GPS tracks of the dolphin-watching boat are available, making it possible to account for spatial bias by weighting the observations based on “survey” effort. If the platform of opportunity models reveal similar patterns to the ones found through standardised surveys, albeit in a smaller area, they could provide even more detailed insight into daily/weekly/monthly movement patterns and behaviours, as the re-sighting rate of individuals is much higher than from the research vessel.

6.4. Common themes identified on different modelling scales

Though each of these studies focused on a different spatial and temporal scale, several common themes emerged from the habitat modelling processes. For instance, in every case, including interactions of environmental covariates with factors describing different states—habitat type, site, tidal phase—identified features that would otherwise not have been observed. In the large spatial scale models (Chapter 2), habitat-specific responses to the same suite of predictors were found. In the intermediate models (Chapter 3), not only were site-specific differences in dolphin presence observed, but also temporal scale-specific

differences in model performance. And finally, grouping observations by tidal state in the fine-scale models (Chapter 4) revealed spatial patterns, namely, the significance of the bottleneck feature in the Shannon Estuary, that would not have been apparent otherwise.

Another recurring theme was the low percentage of observed deviance explained by several of the models tested. There are a number of factors at play here. Firstly, the behavioural plasticity of the species being modelled means that it may show variable responses to the same environmental parameters, weakening the link between predictors and responses. It has been noted that species with restricted tolerance for environmental fluctuations and limited distributions are generally well predicted by models (Tsoar et al., 2007). Bottlenose dolphins are tolerant to a wide range of environmental parameters, as is evident by their cosmopolitan distribution. On top of that, Jiménez-Valverde, Lobo, & Hortal (2008) argue that species with a small relative occurrence area (ROA, the extent of their distribution compared to the extent of the study area) leads to better model fit than for species with higher ROA. By that definition, dolphins in the present studies were sighted throughout the extent of the respective survey areas, giving them a high ROA score and thus confounding model validation techniques. Secondly, bottlenose dolphins are top predators in complex food webs, so their response to changes at lower trophic levels is more indirect than, say, the response of krill-feeding whales to changes in plankton concentration (e.g., Herr et al., 2016). Many of the predictor variables in the models used here are proxies for prey abundance and distribution, and this introduces an added layer of uncertainty to the models—something the inclusion of actual prey distribution data would minimise. It is also highly likely that critical environmental or behavioural processes were omitted from the models because data were lacking or we simply do not know how they might affect dolphin distribution. This limits the explanatory power of regression-based models; for marine mammals, especially, common values for deviance explained are below 50%, often even below 25% (D. Palacios et al., 2013). Physical factors cannot always be linked directly to marine mammal distribution, while factors that may also play an important role, including social and behavioural processes (e.g., Krützen et al., 2005; Gurarie, Andrews, & Laidre, 2009) are not often included in these models. Moreover, it becomes particularly difficult to incorporate them in a meaningful way, considering that all of these processes may occur at scales of metres to thousands of kilometres (Palacios et al., 2006, 2014). Thirdly, the nature of the available observations themselves, with the comparatively low ratio of detections to non-detections (not absences *per se*, since we cannot rule out presence merely because we did not see or hear dolphins), causes

overdispersion problems for all the models considered. Several error distribution families were tested in each case prior to selecting the best-fitting ones, and yet the final models were still not always able to overcome this issue. This is a recurring issue in cetacean distribution studies, due to their low detectability (not spending much time at the surface, not constantly echolocating, etc.) and several attempts have been made to counter-balance it (e.g., MacKenzie et al., 2002; Monk, 2014; Virgili et al., 2017). Indeed, some of these approaches (such as using a Tweedie distribution) were attempted in the present study but were computationally prohibitive.

The overarching theme of the present thesis would appear to be “look more closely.” When it comes to detecting and predicting bottlenose dolphin presence, the temporal scale of events is clearly as or more important than the spatial scale. Different predictors affect species at varying scales (Fernandez et al., 2018), and important mechanisms that drive dolphin habitat preferences and site occupancy would have been missed had patterns from hourly to seasonal observations not been investigated. This further highlights the value of long-term studies, as they provide us with sufficient observations to be divided into smaller categories (e.g., winter/summer, spring/neap) without reducing the available observations too much for the models to converge. (This effect was noticeable, for instance, when attempting to run the models outlined in Chapter 4.2 on the winter dataset; very few winter surveys took place in the Shannon, resulting in a low number of dolphin encounters and non-converging models. See also Appendix IIB.) Increasing survey and monitoring effort in all areas and seasons would greatly enhance our ability to conduct more detailed investigations of habitat use.

6.5. Concluding remarks

The conservation implications of these findings are manifold. For one thing, while it has been previously shown that the bottlenose dolphin populations studied here do not significantly overlap genetically, demographically, or geographically, it is now clear that they also differ in their habitat preferences. This further supports the hypothesis that they form distinct ecotypes (Oudejans et al., 2015) and should be treated as discrete management units, as, indeed, is outlined by the JNCC (IAMMWG, 2015). While the resident population in the Shannon Estuary has been monitored for a long time, as part of the reporting scheme required by the EU Habitats Directive, our obligation to maintain this species’ favourable condition elsewhere in Irish waters cannot be fully met without

more detailed investigation of the distribution, habitat preferences, and abundance throughout each population's range. Having identified some critical features that each population associates with, it will be easier to create targeted studies, as suggested in each chapter and the present discussion, in order to investigate ranging patterns, foraging strategies, and abundance monitoring in each area. Moreover, using a platform of opportunity as a means to survey the resident population when standardised surveys do not take place will not only increase our ability to detect population trends in a timely fashion, but also to collect detailed demographic information that is still, despite years of monitoring effort, lacking and arguably more important. This is the first comprehensive attempt to investigate bottlenose dolphin habitat use and site occupancy across the Irish seaboard and these findings will hopefully serve as a baseline to address critical questions and design appropriate conservation and management plans.

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“Even top predators get eaten sometimes”

—Larry



Photo: Lucy Taylor

FJN